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Understanding the depredation process in grey wolf (*Canis lupus*) and its interactions with lethal measures: focus on the French Alpine Arc

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et **Simon CHAMAILLÉ-JAMMES**

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Avant-propos

Ce travail de thèse s'est penché sur les prédations par le loup gris (*Canis lupus*) sur les troupeaux domestiques, et sur la modification de ces prédations, aussi appelées déprédations, provoquée par le contrôle létal appliqué au prédateur. J'ai utilisé trois études complémentaires. La première explore l'effet général du contrôle létal selon le comportement de déprédation du loup grâce à une simulation sur ordinateur. La deuxième analyse spécifiquement l'effet des tirs de loup sur les déprédations en France. Enfin, la dernière évalue l'évolution de l'agrégation des attaques dans l'arc alpin. Je montre que la déprédation est un phénomène complexe, dépendant du loup lui-même mais aussi d'autres facteurs environnementaux et pastoraux. Plus spécifiquement aux mesures létales, j'en conclus que leurs effets sont dépendants des contextes locaux et que ces derniers doivent être considérés pour la gestion des attaques et la réduction des conflits.

Vous trouverez dans cette thèse une introduction qui récapitule le contexte de la conservation du loup à travers le prisme de la gestion de ses attaques sur les troupeaux, en focalisant surtout sur la France, mais en évoquant aussi les situations en Europe et aux Etats-Unis. Suivront ensuite les trois études mentionnées ci-dessus, sous la forme de chapitres. Je me suis attachée pour chacun d'eux à fournir une synthèse de la littérature scientifique, non seulement pour partager les connaissances déjà acquises sur le sujet, mais également pour éviter les idées reçues. Une discussion générale conclut la thèse.

Ce document est la version mixte anglaise-française de la thèse. L'essentiel de la thèse y est rédigé en anglais, mais vous pouvez trouver un résumé et une synthèse en français en début et en fin de document.

Parce qu'il n'est pas toujours évident de lire une thèse en intégralité, je vous propose de guider votre lecture selon vos points d'intérêt. Si vous êtes intéressés par l'un des points suivants, vous pouvez aller à la partie indiquée à sa droite (en cliquant dessus pour la version électronique, ou en allant à la page mentionnée sinon).

1. La synthèse :
    a) Un résumé d'une page de l'intégralité de la thèse ➙ Résumé page vi
    b) Une synthèse détaillée de la thèse, de son positionnement, ses résultats et recommandations ➙ Chapter 5 (Discussion) on page 223
2. Le contexte de la thèse :
    a) Une mise en contexte sur les relations entre l'Homme et le loup ➙ section *The complicated relationship between wolves and humans* on page 2
    b) Une description brève des contextes de déprédations aux Etats-Unis, en Europe et en France ➙ section *Different contexts of depredation* on page 7
    c) Une description des mesures de gestion des déprédations, avec une description de l'actuelle application administrative en France ➙ section *The tools of the management of depredation* on page 11
    d) Les objectifs de la thèse ➙ section *Context, objectives and collaborations* on page 27
3. Les connaissances scientifiques :
    a) La dynamique naturelle d'une population de loups ➙ section *The wolf population dynamic without culling* on page 33
    b) La perturbation de cette dynamique par les mesures létales ➙ section *Wolf population dynamic disruptions* on page 37
    c) Le comportement de prédation du loup ➙ section *Literature review* on page 59
    d) L'effet du contrôle létal sur les déprédations ➙ section *Literature review* on page 128
    e) Les méthodes pour identifier les points chauds de déprédation ➙ section *Literature review* on page 204
4. Mes propositions méthodologiques :
    a) Modélisation d'une population de loups ➙ section *Modelling* on page 39

b) Modélisation du comportement de déprédation ➙ section *Modelling* on page 81
c) Analyse de l'effet du contrôle létal sur les attaques observées en France ➙ section *Analysis* on page 143
d) Identification des points chauds en tenant compte de la distribution des moutons en France ➙ section *Analysis 2: Wolf depredation hotspot location* on page 212

5. Mes résultats :
   a) Effets du contrôle létal sur la population modélisée de loups et sur ses déprédations ➙ section *Interpretation of the results* on page 115
   b) Ma synthèse du possible comportement de déprédation en France selon les résultats de modélisation ➙ section *A French scenario?* on page 117
   c) Effets des tirs de loup en France selon le contexte ➙ section *Variability of the culling effects* on page 170
   d) Agrégation générale des attaques de loups en France ➙ section *Analysis 1: Summarised spatial structure of wolf depredations* on page 214
   e) Identification des points chauds de déprédation en France ➙ section *Analysis 2: Wolf depredation hotspot location* on page 216

Si vous lisez la thèse au format électronique, alors vous pourrez constater que les références bibliographiques ou les références aux sections, figures, ou tableaux, sont interactives. L'introduction, les chapitres et la discussion peuvent se lire indépendamment, et il peut donc y avoir des redondances entre ces parties.

J'ai essayé de rendre la lecture de cette thèse la plus fluide possible et accessible même aux personnes non-initiées à la biologie des populations ou à celle du loup. J'espère qu'elle pourra être utile à d'autres études et à la gestion des attaques de loups dans un but de conservation du loup gris par la réduction des conflits.

En vous souhaitant une bonne lecture !

Oksana Grente

Foreword

This thesis examined the predations by the grey wolf (*Canis lupus*) on livestock, and how these predations, also called depredations, were modified by lethal control applied on the predator. I used three complementary studies. The first one explored the general effect of lethal control according to the wolf depredation behaviour, thanks to computer simulations. The second one specifically analysed the effects of wolf culling on depredations in France. Finally, the last study evaluated the changes of aggregation of depredations in the French Alpine Arc. Overall, I showed that depredation is a complex process, depending on the wolf itself, but also on other environmental or pastoral factors. More specifically to the lethal measures, I concluded that their effects were depending on local contexts and that these contexts should be considered for depredation management and mitigation of conflicts.

You will find in this thesis an introduction which sums up the wolf conservation context through the prism of depredation management, by mostly focusing on France, but also by mentioning the situations in Europe and in the United States of America. The three previously mentioned studies then follow in the form of chapters. I sought to provide, for each chapter, a synthesis of the scientific literature, not only to share existing knowledge, but also to avoid misconceptions about the subject. A general discussion then conclude the PhD thesis.

This document is the English-French hybrid version of the thesis. Most of the thesis is written in English, but there is also an abstract and a synthesis at the beginning and at the end of the document in French.

Because it is not always easy to read a thesis in its entirety, I propose guiding you throughout the thesis according to your interest. If you are interested by one of the following points, you can go directly to the mentioned section (by clicking directly on it for the electronic version, or by going to the mentioned page otherwise).

1. The synthesis:
    a) A one-page abstract of the whole thesis ➙ Abstract page vii
    b) A detailed synthesis of the thesis, its positioning regarding the controversy of wolf culling, its results and its recommendations ➙ Chapter 5 (Discussion) on page 223
2. The context of the thesis:
    a) The background of human-wolf relations ➙ section *The complicated relationship between wolves and humans* on page 2
    b) A brief description of the contexts of depredations in the USA, Europe and in France ➙ section *Different contexts of depredation* on page 7
    c) A general description of the management tools of depredations, and a description regarding their administrative implementations in France ➙ section *The tools of the management of depredation* on page 11
    d) The thesis objectives ➙ section *Context, objectives and collaborations* on page 27
3. The scientific knowledge:
    a) The natural dynamic of wolf population ➙ section *The wolf population dynamic without culling* on page 33
    b) The disruptions of this dynamic by lethal control ➙ section *Wolf population dynamic disruptions* on page 37
    c) The wolf depredation behaviour ➙ section *Literature review* on page 59
    d) The effect of lethal control on depredations ➙ section *Literature review* on page 128
    e) The methods for depredation hotspot identification ➙ section *Literature review* on page 204
4. My methodological propositions:
    a) Wolf population modelling ➙ section *Modelling* on page 39

b) Depredation behaviour modelling ➙ section *Modelling* on page 81
c) Analysis of the effect of wolf culling on depredations observed in France ➙ section *Analysis* on page 143
d) Identification of hotspots adjusting for sheep distribution in France ➙ section *Analysis 2: Wolf depredation hotspot location* on page 212

5. My results:
   a) The effects of lethal control on the modelled population of wolves and on its depredations ➙ section *Interpretation of the results* on page 115
   b) My synthesis about the potential depredation behaviour in France regarding the modelling results ➙ section *A French scenario?* on page 117
   c) The effects of wolf culling in France according to contexts ➙ section *Variability of the culling effects* on page 170
   d) The summarised depredation clustering pattern in France ➙ section *Analysis 1: Summarised spatial structure of wolf depredations* on page 214
   e) The identification of hotspots in France ➙ section *Analysis 2: Wolf depredation hotspot location* on page 216

If you read the thesis with the electronic format, then you will see that literature references or mentions to sections, figures or tables are interactive. The introduction, the chapters and the discussion can be read independently to each other, explaining why there can be some redundancy between these parts.

I tried to make the reading of this thesis as flowing as possible, and accessible to people not so familiar with wolf or with population biology.I hope my thesis will be useful to studies to come and to the management of depredations of wolves, with the aim of the conservation of the grey wolf through the reduction of conflicts.

Wishing you a pleasant reading!

Oksana Grente

Résumé

Après sa disparition de France dans les années 1950, le loup gris (*Canis lupus*) est revenu et est désormais installé à travers tout l'arc alpin. Ses prédations sur le bétail, appelées déprédations, ont augmenté depuis la recolonisation de cette région. Elles concernent surtout les moutons dans le contexte du pastoralisme. Ce phénomène crée des conflits entre la conservation du loup et les activités pastorales. En plus des indemnisations et des subventions pour les mesures de protection des troupeaux, la France a ajouté un autre outil de gestion des ces conflits, les prélèvements létaux de loups.

L'incertitude persiste au sujet de l'efficacité des mesures létales pour réduire la déprédation, que cela soit en France ou ailleurs où elles sont appliquées. Deux hypothèses contradictoires s'opposent. La première soutient que les mesures létales sont efficaces grâce à la réduction de la population et la sélection de loups moins enclins à la déprédation. La deuxième hypothèse soutient que ces mesures sont contreproductives à cause de la déstabilisation des meutes qui engendre une augmentation de la dépendance des loups vis-à-vis du bétail.

La raison de cette incertitude est la combinaison d'un faible nombre d'études sur le sujet et d'une faible inférence scientifique, qui conduit à des résultats contradictoires. De plus, la majorité des études s'est concentrée sur la situation nord-américaine. Mon travail consistait à réduire l'incertitude de l'effet des mesures létales sur les déprédations réussies et observées sur les moutons en France.

Nous avons adopté deux approches. Premièrement, **nous avons choisi une approche de modélisation individu-centrée pour étudier la dynamique complète des mesures létales sur la structure de la population de loups et sur les déprédations**. Nous avons intégré des mécanismes biologiques, tels que la dissolution des meutes. Nous avons testé différents scénarios de comportement de déprédation des loups. Notre modèle soutient que les mesures létales modélisées étaient efficaces pour réduire les déprédations par la réduction de la population 1) quand la probabilité de déprédation augmentait pour les loups en meute à cause de besoins énergétiques plus élevés ou 2) quand, en plus, elle augmentait aussi pour les loups adultes et avec la taille de la meute. En revanche, notre modèle ne nous a pas permis de conclure sur les effets des mesures létales quand les probabilités de déprédation diminuaient pour les adultes ou avec la taille de la meute.

Deuxièmement, **nous avons analysé les effets de la mort de loups sur les niveaux de déprédation en France avec les données de l'administration**. Nous avons développé une méthodologie basée sur les calculs par noyaux. Nous concluons que les effets des tirs en France ont été hautement variables selon le contexte d'application. En majorité, une réduction de l'intensité de la déprédation a été constatée suite aux tirs, mais pouvaient aussi être observées une absence d'effet ou bien une augmentation.

Enfin, **nous avons ajouté une analyse rétrospective de la répartition spatiale des déprédations en France, que l'on a ajustée par les distributions spatio-temporelles des moutons ainsi que par la taille de leurs troupeaux**. Nous concluons que les points chauds de prédation ne résultaient probablement pas du seul facteur de la territorialité des loups. Nous observons que la déprédation s'homogénéisait au fil du temps dans l'arc alpin. La méthode nous a permis de repérer les points chauds avec de petits troupeaux ou pâturant peu de temps qui n'auraient pas été détectés avec l'actuelle méthode appliquée par l'administration.

Ainsi, ce travail montre que le contexte local lié à l'environnement, au loup et au pastoralisme a besoin d'être considéré pour la gestion des déprédations, car il est peu probable que les tirs de loup aient un effet unique sur les loups et la déprédation dans tous les contextes.

Abstract

After its disappearance from France around the 1950s, the grey wolf (*Canis lupus*) has returned and is now settled throughout the French Alpine Arc. Its predations on livestock, called depredations, have increased across time since its recolonisation of the region. Depredations mostly concern sheep within the context of pastoralism. The depredation process creates conflicts between wolf conservation and pastoral activities. Besides financial compensations of depredation losses and subsidies for non-lethal protective measures of flocks, France has added another tool of mitigation: lethal removals of wolves.

Uncertainty remains about the efficiency of lethal measures to reduce the depredations levels, whether it is in France or elsewhere where these measures are applied. Two opposite assumptions are currently made. The first assumption supports that lethal measures are efficient through population reduction and selection of wolves less likely to depredate. The second assumption supports that lethal measures are counter-productive because of pack disruption which in turn increase the needs of wolves to rely on livestock.

The reason for the uncertainty about the effects of lethal measures is the combination of a low number of studies on the subject and a weak scientific inference, thus producing contradictory results. Moreover, most studies have focused on the North American situation. My work consisted in reducing the uncertainty about the effects of lethal measures on the recorded successful depredations on sheep in France.

We adopted two approaches. First, **we developed an individual-based modelling approach to study the whole dynamic induced by lethal measures on the wolf population structure and on depredations**. We integrated biological mechanisms as pack dissolution that were never integrated before. We tested different scenarios of depredation behaviour of wolves. Our model supported that the modelled lethal measures were efficient to reduce depredations through population size reduction 1) when the individual probability of depredation was increasing for wolves in pack because of increasing food needs or 2) when, in addition, it was also increasing for adult wolves and with pack size, to mimic hunting abilities. On the other hand, our model did not allow us to conclude on the effects of lethal measures when the individual probability of depredation was decreasing for adults or with pack size.

Second, **we analysed the effect of the deaths of wolves on the depredation levels in France with data provided by the French administration**. We developed a methodology based on kernel calculations. We concluded that the effect of culling in France was highly variable according to contexts. The majority of the results involved a reduction of the depredations, but could also involve no effect or an increase of the depredations.

Finally, **we added a retrospective analysis of the depredation spatial pattern in France by adjusting for spatial and temporal sheep distributions and flock sizes**. We concluded that hotspots likely did not result from the unique factor of wolf territoriality. We also observed that depredations tended to homogenise across time in the French Alpine Arc. The method finally allowed us to spot hotspots encompassing small flocks or grazing over a short period, which would have remained unspotted with the current hotspot determination of the French administration.

Thus, this work shows that the local context, linked to environmental, wolf and pastoral variables, needs to be taken into consideration for the management of depredations, because lethal measures are unlikely to have a unique effect on wolves and their depredations.

Remerciements

J'ai du mal à réaliser que mes trois années et quelques mois de thèse s'achèvent en cette fin 2021. Même entachées d'une pandémie mondiale, ces trois années furent trois années de bonheur et d'épanouissement, sur le plan professionnel comme sur le plan personnel. Dans les moments faciles comme difficiles, j'ai pu trouver du réconfort, de l'aide et du soutien. Ma thèse est avant tout un travail collectif. Aucune des études présentées dans ce manuscrit n'a été réalisée par moi seule. Etudier le loup, et encore plus les tirs de loup, est un sujet prenant, parfois envahissant. Seul le soutien inconditionnel de mes proches et de mes superviseurs, collègues et collaborateurs m'a permis de conserver un équilibre indispensable pour mener à bien cette thèse. Par conséquent, cette thèse ne peut commencer sans remercier toutes ces personnes. Je m'excuse par avance des possibles oublis.

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Que serait une thèse sans le soutien des amis et de la famille ? Sans eux, je n'aurais pas pu tenir le cap. Ils ont su me réconforter, m'aider pour la thèse mais aussi, et c'est tout aussi important, me faire déconnecter.

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Introduction

Introduction

Three actors are at the centre of my work: humans, domestic sheep and grey wolves. This work focused on the interactions of these three actors, with a special attention to the situation in France, and more precisely in the French Alps, in the south-east of the country.

If I may, I will skip the presentation of the first actor *Homo sapiens* and will rather give a brief introduction of the second and third ones.

The domestic sheep *Ovis aries* is a species from the *Bovidae* family, itself part of the *Artiodactyla* order [1]. It is with goats the first livestock species to be domesticated, first for meat, then for wool [2]. They are currently found on every continent [3]. In France, 59 official sheep breeds are currently found [4], totalling around 7 millions of farmed sheep used for meat or for milk [5].

The grey wolf *Canis lupus* is a species from the *Canidae* family, itself part of the *Carnivora* order [1]. Currently, the species can be found over a large range in the Northern hemisphere, from Greenland to India, and is present both in North America and Eurasia. There is no past or current record of the species below the equator [6]. In France, the population is estimated at 624 individuals (with a confidence interval of 414-834) and 106 packs at the beginning of 2021.

Now that the introductions have been made, I will go into deeper details about the interactions of these three actors. These interactions will be presented at the global scale, generally with a focus on Europe[1] and North America[2] and then at the scale of interest, France, and more precisely, the French Alpine Arc. The aim of this section is to go through the current management of predations of wolves on livestock, especially in France, with a special focus on lethal measures.

[1]: Linnaeus (1758), *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis.*

[2]: Chessa et al. (2009), 'Revealing the History of Sheep Domestication Using Retrovirus Integrations'

[3]: Gilbert et al. (2018), *Global Sheep Distribution in 2010 (5 Minutes of Arc)*

[4]: Ministère de l'Agriculture (2015), *Arrêté Du 29 Avril 2015 Fixant La Liste Des Races Des Espèces Bovine, Ovine, Caprine et Porcine Reconnues*

[5]: IDELE (2019), *Ovins 2019 Productions lait et viande*

[6]: Boitani et al. (2018), *Canis Lupus (Errata Version Published in 2020)*

1: It is essential to understand the French context

2: Most of the scientific literature about wolf predation on livestock and wolf biology is focused on this continent, and its situation is often compared to the one in France.

The complicated relationship between wolves and humans

From campaigns of destruction...

As for many other large predators worldwide, the coexistence between *Canis lupus* and humans is challenging. Apart from the direct threats these predators might present for human safety, they might be seen as competitors for food, whether it is wild or domestic [7].

Historically, part of humans responded to theses challenges by hostility, especially in Europe [8]. In this regard, *Canis lupus* is a good illustration. The species has been the subject of planned campaigns of destruction [9]. Charlemagne, King of Franks in the eighth century, formalised a specific group of men designated to eradicate the animals considered as pest [10]. These men were called *luparii* in Latin or *louvetiers* in French, from the etymology *lupus* or *loup* which designates the wolf, because more

[7]: Lute et al. (2018), 'Conservation Professionals Agree on Challenges to Coexisting with Large Carnivores but Not on Solutions'

[8]: Fritts et al. (2003), 'Wolves and Humans.'

[9]: Boitani (2003), 'Wolf Conservation and Recovery'

[10]: Moriceau (2011), *L'Homme Contre Le Loup: Une Guerre de Deux Mille Ans*

than any other pest, the grey wolf was the target [11]. It must be said that this species had a bad reputation in the Middle Ages in Europe, being considered as the incarnation of the devil on Earth by Christianity, and as a danger for humans beings represented as sheep [8, 11]. This belief was exported to North America during the Age of Discovery several centuries later, and the persecutions too [9]. Up to the twentieth century, the grey wolf was still persecuted [12, 13], bounties being paid to hunters in certain areas when killing wolves (*i.e.* up to 1947 in Oregon, USA [14], up to 1975 in Poland [15]). In an encyclopaedia directed by a professor from the National Museum of Natural History of Paris, dated from 1950 and aimed at the general public, you can read about the grey wolf '[...] *the Wolf is everywhere an undesirable denizen of forests and steppes. It is not very crafty or very brave, but it is patient and tenacious. Its prudence enables it to avoid many traps.*' [16], p.408.

[11]: Collin (2021), *Un Jour Est Née La Louveterie*

[12]: Landry (2017), *Le Loup*
[13]: de Beaufort (1987), *Le Loup En France: Éléments d'écologie Historique*

[14]: Hamilton et al. (2020), 'Wolves Are Back: Sociopolitical Identity and Opinions on Management of Canis Lupus'

[15]: Niedziałkowski et al. (2020), 'What Makes a Major Change of Wildlife Management Policy Possible? Institutional Analysis of Polish Wolf Governance'

[16]: Bertin (1950), *Les Mammifères - Loups.*

The hatred towards *Canis lupus* had not always been that extreme in other places or in other times. Native Americans can be described as traditionally regarding wolves as a model [17], and '*rarely killing wolves*' [12], p.315, even if the review of [8] partly contradicts this view, where it is said that wolf hunting was common among many tribes, notably for furs, but never in an attempt to exterminate the species. In Kyrgyzstan, wolves are seen as an alter-ego rather than pest, but can be killed by humans if they intrude the human lands and pastures, in order to ensure an '*equilibrium*' between wolves and humans [18].

[17]: Fogg et al. (2015), 'Relationships Between Indigenous American Peoples and Wolves 1: Wolves as Teachers and Guides'

[18]: Lescureux (2007), 'Maintenir La Réciprocité Pour Mieux Coexister ?Ethnographie Du Récit Kirghiz Des Relations Dynamiques Entre Les Hommes et Les Loups'

The efficiency of the campaigns of destruction in Europe and in North America, combined to the loss of natural habitat [19], led to a massive decline of their wolf populations and to range restrictions in the end of the twentieth century. Once widespread to Mexico, the grey wolf only remained in the Northern section of its range in North America, in Canada and in Alaska, with several hundreds of individuals remaining in Minnesota for the Contiguous United States [9].

[19]: Wolf et al. (2017), 'Range Contractions of the World's Large Carnivores'

In Europe, the species was extirpated from most of Western Europe essentially during the nineteenth century [6]. In France, the documented drop in the wolf's range in only one century was quite spectacular (Figure 0.1 [13]). The easier access to hunting and the acceleration in the efficiency of hunting techniques, combined to a continuous effort to exterminate the species, were probably the reasons of this drop [12]. The last settled wolves in France were killed in 1929 in the Centre-West remaining pocket (Figure 0.1.c).

In the French Alps, the grey wolf disappeared at the beginning of the twentieth century (Figure 0.1.c). In the following decades, the closest wolves from the Alps were the remaining wolves in Italy, found in small numbers in restricted areas of the Central and South Apennines [20], the

[20]: Zimen et al. (1975), 'Number and Distribution of Wolves in Italy'

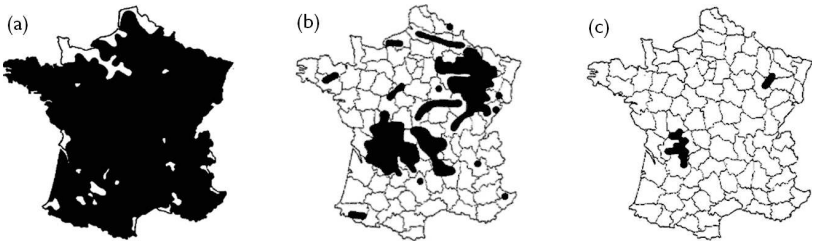


Figure 0.1: Documented wolf distribution (black spots) in France in (a) the end of the eighteenth century (b) the end of the nineteenth century and (c) around 1923. Credits: De Beaufort, 1987 [13]

population found in the Dinaric Alps in Slovenia [9], and the population in the northwest of Spain [21] (Figure 0.2).

[21]: Chapron et al. (2014), 'Recovery of Large Carnivores in Europe's Modern Human-Dominated Landscapes'

...to full protection...

From the 1970s, the tide has been turning in the favour of *Canis lupus* in Europe [22] and in North America [23] for several reasons. First, there was a turnaround of the legislation and of the public opinion: the wolf shifted from pest to valuable species that needs protection [21]. In Europe, the grey wolf has been part of the Annex II of the Bern convention (1979), and later of the Annex IV of the Habitats Directive (1992), therefore benefiting from a full protection status (*i.e.* no killing allowed). In the USA, the species has been listed in the Endangered Species Act (1973) and has benefited from the same protection[3] and from reintroductions into the Yellowstone National Park and central Idaho in 1995 and 1996[4]. Second, the loss of natural habitat halted, and ungulate populations and forested areas have raised during the last few decades [25, 26].

[22]: Louvrier (2018), 'Modélisation statistique de la distribution des grands carnivores en Europe'

[23]: Ripple et al. (2014), 'Status and Ecological Effects of the World's Largest Carnivores'

3: There has been multiple policy changes regarding its protection since then [24].

4: See 'Wolf Recovery in North America' by the US Fish and Wildlife Service

[25]: Beguin et al. (2016), 'Management of Forest Regeneration in Boreal and Temperate Deer–Forest Systems: Challenges, Guidelines, and Research Gaps'

[26]: Carpio et al. (2021), 'Wild Ungulate Overabundance in Europe: Contexts, Causes, Monitoring and Management Recommendations'

[27]: Poulle et al. (1999), 'La recolonisation des Alpes françaises par le loup de 1992 à 1998'

These conditions allowed a recovery of the grey wolf in both Europe and North America, with a demographic increase and geographic expansion (Figure 0.2). Wolves from the Apennines population migrated towards the Western Alps and progressively recolonised this area. In 1992, two wolves were seen together in the Mercantour National Park (MNP) in the department of Alpes Maritimes [27], by two guards of the park, Patrick Orméa and Anne-Marie Issautier. The observation has been relayed for the first time in a French magazine in 1993, with the title '*Welcome*

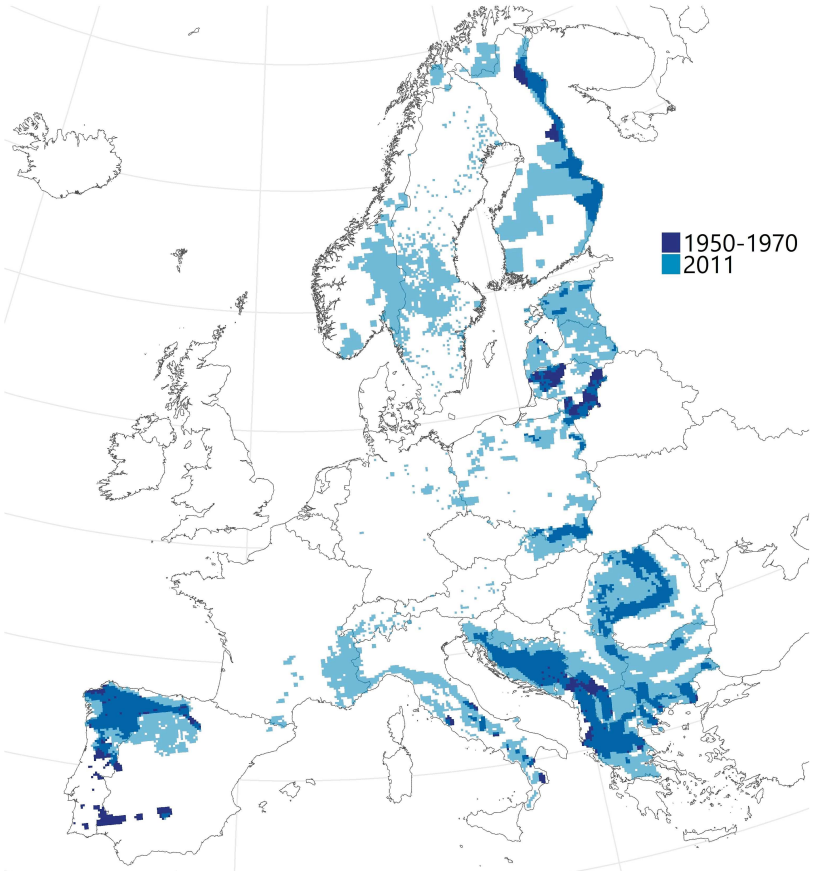


Figure 0.2: Estimated wolf distribution in Europe during the 1950s-1970s and in 2011. The sporadic and permanent distributions in 2011 have been grouped together. Credits: O. Grente. Data: Chapron *et al.*, 2014 [21]

to the wolf' (Figure 0.3). Quite contrasting with the wolf undesirability mentioned in the encyclopaedia article cited earlier [16].

From the MNP, the grey wolf rapidly recolonised the rest of the French Alps [28] (Figure 0.4). The furthest Alpine department from the MNP, Haute-Savoie, has been durably recolonised by wolves since 2003 [28]. Since 1992, the number of reproductive packs has progressively increased in the French Alpin Arc. At the end of 2020, 105 reproductive packs were counted in this area [29]. The new packs have been filling the interstices between the existent packs, and the area is now densely filled with packs [29].

All wild wolves found in the French Alps since the recolonisation of the species have the same genetic lineage than the Italian wolves from the Apennines, which are part of the grey wolf subspecies *Canis lupus italicus* (Altobello, 1921). However, the Alpine population, which overlaps Italy, France and Switzerland [21], is distinct from the Apennines population, both populations being connected by a narrow corridor which allows a reduced gene flow [30].

Wolves from the Alpine population reached the Vosges, in Northeast of France, as soon as 1995, which is not surprising given the known capacity of dispersal at large distances of this species [31]. However the first attested reproduction in this zone only happened in 2013 [32]. Other individuals from the Alps reached the Massif Central in 1998, but the settlement has only been stable around 2007-2009. Currently there is still no attested pack in this area [28]. A similar scenario is occurring in the Pyrenees mountains: early observations of wolves coming from the Alps were reported in 1999, who settled in the area, but there is still no attested pack at this time [28]. Some lone wolves also settled in the interstices of these two zones, in Tarn and Hérault around 2008 [28]. Erratic observations were made in the rest of the country, up to Normandy (north-west) in 2020 [33] or along the Atlantic coast in 2021. Outside the Alps and the Vosges, most of these lone wolves were or are males (M. Petit, OFB, *pers. com.*). In 2021, there is no reproductive pack outside the Alps in the country, except one pack in Jura, to the North of the Alps [29].

No wolf from the Iberian population, part of another subspecies, *Canis lupus signatus* (Cabrera, 1907), was found in France at this time. This is possibly consistent with the short estimated dispersal distances for this subspecies [34, 35]. The only individual known to have naturally dispersed in France since the 90s and that was not part of the Alpine population, was a German wolf from the genetic lineage of Central Europe, observed in north-east France in 2020.

...with polarised attitudes

Despite what appears as a favourable public opinion regarding wolves, conflicts between humans and wolves have not ceased. The main driver of this conflict is not the direct threat to human safety. In the USA, attack on humans caused by wolves was subject to the fewest registers compared to the other large predators, such as cougars and grizzlies [37] (note that the study did not correct the analysis with the predator's abundances or risks of encounters with humans). In Europe however, threats to human



Figure 0.3: Front cover of the magazine *Terre Sauvage* in May 1993, '*Welcome to the wolf: it comes back in France*'. It was the first public release about the settlement of wolves in France after the species extinction in the first part of the twentieth century. Article available in French here. Authors of the article: Geneviève Carbone and Antoine Peillon.

[28]: Office Français de la Biodiversité (2021), *Portail Carmen - Loup Gris*

[29]: Réseau Loup-Lynx (2021), *Bilan de suivi hivernal de la population de loups - Hiver 2020/2021*

[30]: Fabbri et al. (2007), 'From the Apennines to the Alps'

[31]: Mech et al. (2003), *Wolves: Behavior, Ecology, and Conservation*

[32]: Loup-Lynx (2013), 'Une Meute d'au Moins 4 Loups Installée Dans Les Vosges'

[33]: Réseau Loup-Lynx (2020), *Bilan de suivi estival de la population de loups - été 2020*

The French wolf subpopulation

The Alpine population of wolves currently covers the Italian, French and Swiss Alps [21]. Thus, wolves in the French Alps form a subpopulation of the Alpine population. For simplicity, the '*French wolf population*' will be used thereafter to name all wolves from this subpopulation.

[34]: Blanco et al. (2007), 'Dispersal Patterns, Social Structure and Mortality of Wolves Living in Agricultural Habitats in Spain'

[35]: Nakamura et al. (2021), 'Source-Sink Dynamics Promote Wolf Persistence in Human-Modified Landscapes: Insights from Long-Term Monitoring'

[37]: Garrote et al. (2017), 'Individual Attributes and Party Affect Large Carnivore Attacks on Humans'

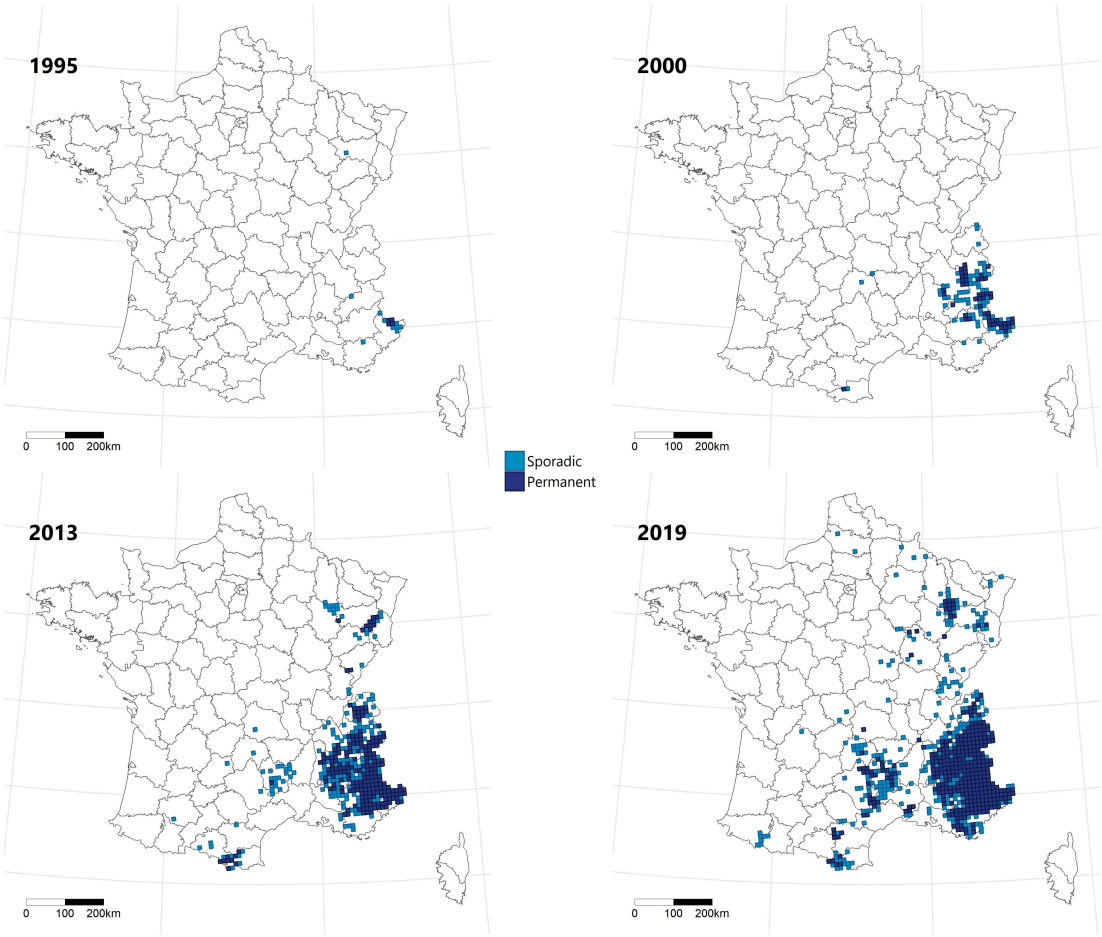


Figure 0.4: Observed wolf distributions in France in 1995, 2000, 2013 and 2019, on cells of 10×10 km. A permanent cell in year y means that at least two verified observations have been made from April $y-3$ to March $y-2$, and from April $y-1$ to March y in the cell. A sporadic cell in year y means that the previous condition was not fulfilled, but that at least one observation was made in the cell during the two biennial periods [36]. Source: OFB [28]. Credits: O.Grente

safety caused by wolves are controversial, and the presence of '*fearless*' or '*bold*' wolves is admitted in the academic world [38, 39]. Risks of attack of wolves on humans are considered '*above zero, but far too low to calculate*' [40].

The main driver of conflict between wolves and humans is competition with humans for prey. The prey can be wild. For example in Finland, where the elk (*Alces alces*) hunting culture is important, the heavy reliance of wolves on this species explains the negative attitudes towards wolves from hunters, in addition to what is perceived as a high risk for hunting dogs due to the wolf's presence [41].

But generally, the competition for prey between humans and wolves involves domestic prey. Predation of large predators on domestic prey is called **depredation**. This is the first source of conflict cited by conservationists when pooling all species of predators [7]. Depredations were the main reason of the campaigns of destruction of wolves in the last centuries [8]. In Europe, farmers are the stakeholder group with the most negative attitudes regarding wolves, before hunters. In Norway, Sweden and Finland, the wolf is hunted in the reindeer herding areas [41] [42].

The conflicts due to competition for domestic and wild prey do not

[38]: Linnell et al. (2016), 'Predators That Kill Humans: Myth, Reality, Context and the Politics of Wolf Attacks on People'

[39]: Reinhardt et al. (2020), *How to Deal with Bold Wolves*

[40]: Linnell et al. (2021), *Wolf Attacks on Humans: An Update for 2002–2020*

[41]: Bisi et al. (2010), 'The Good Bad Wolf—Wolf Evaluation Reveals the Roots of the Finnish Wolf Conflict'

[42]: Milleret et al. (2017), 'Let's Stay Together?'

trigger negative attitudes only in the groups of stakeholders directly affected by it. In North America, negative contents regarding wolf's conservation drastically decreased in the media between 1999 and 2001, but progressively increased, thus overwriting the positive contents [43]. In Europe, a meta-analysis showed that the mean general public positive attitude towards wolves was only of 54% between 1976-2012, demonstrating division in society [44]. This appears in contradiction with what is generally depicted as a large public acceptance of wolves [21].

The division seemed very polarised, with *pro-wolf vs. anti-wolf* groups as mentioned in Sweden [45]. In Finland, there is a strong demand from the general public to open wolf hunting[5]. This demand occurs despite multiple lawsuits involving Finland, local nature protection organisations and the European Court of Justice. These lawsuits all turned into Finland's disadvantage [46].

In Europe, the negative attitudes seemed to increase with the duration of the wolf's settlement in the stakeholder's area [44] (note that the media coverage in North America showed the opposite [43]). In Germany, the negative attitudes have been showed to decrease with the level of knowledge about wolves. They also depended on sources of information, the news from written press and television significantly triggering more negative attitudes than books and films [47]. In France, the attitudes triggered by the written press could also depend on the type of press. [48] showed that *Le Monde*, a national journal, covered the conflict by putting forward the needs for wolf conservation, whereas *Nice-Matin*, a journal from the *Alpes-Maritimes* department[6], put forward the damages on livestock.

[43]: Houston et al. (2010), 'Attitudes Toward Wolves in the United States and Canada: A Content Analysis of the Print News Media, 1999–2008'

[44]: Dressel et al. (2015), 'A Meta-Analysis of Studies on Attitudes toward Bears and Wolves across Europe 1976–2012'

[45]: Lin et al. (2021), 'Modelling Stakeholder Satisfaction for Conflict Resolution in Wildlife Management: A Case of Wolf Population in Sweden'

5: Ilpo Kojola at the LIFE WolfAlps webconference, accessible here

[46]: Epstein et al. (2020), 'Non-Governmental Enforcement of EU Environmental Law: A Stakeholder Action for Wolf Protection in Finland'

[47]: Arbieu et al. (2019), 'Attitudes towards Returning Wolves (Canis Lupus) in Germany: Exposure, Information Sources and Trust Matter'

[48]: Chandelier et al. (2018), 'Content Analysis of Newspaper Coverage of Wolf Recolonization in France Using Structural Topic Modeling'

6: The first department in France where depredations occurred since the wolf recolonisation, and still the department with the highest number of depredations in France. [49]

Different contexts of depredation

The management of conflicts between humans and wolves has appeared along the programs of wolf restoration and conservation. The most challenging aspect of wolf conservation is the management of the depredations made by wolves.

In every country where wolves and livestock co-occur, depredations occur [8]. However, agricultural contexts widely vary across the wolf's range. Depending on the country, the livestock concerned by depredation of wolves can be of multiple types: sheep, cattle, goat, poultry, horse, reindeer, dog and pig [8] [50, 51]. After introducing the agriculture and depredation contexts in the USA and Southern Europe, I will present the French context.

[50]: Fritts et al. (1992), *Trends and Management of Wolf-Livestock Conflicts in Minnesota*

[51]: Imbert et al. (2016), 'Why Do Wolves Eat Livestock?'

[52]: Santiago-Avila et al. (2018), 'Killing Wolves to Prevent Predation on Livestock May Protect One Farm but Harm Neighbors'

The USA

In the USA, there are two main areas where depredations occur: the Northern Rockies Mountains NRM (especially Idaho, Montana, Wyoming) and the Great Lakes region (especially Minnesota, Michigan, Wyoming) [31] [52].

In Minnesota and Michigan, the livestock productions vulnerable to wolf predation are the productions of cattle, sheep and turkey [50]. In the

Table 0.1: Counts in 2020 of the main livestock vulnerable to wolf depredation in Minnesota (MN), Michigan (MI), Wyoming (WY), Idaho (ID) and Montana (MT). M stands for million, k for 1 000. Data: [53]

	MN	MI	WY	ID	MT
Cattle	2M	1.1	1.3	**2.5M**	2.45M
Sheep	113k	87k	**340k**	230k	200k
Turkey	**40M**	5.2M	∅	∅	∅

NRM, both cattle and sheep are represented too but not turkey [53] (Table 0.1).

The pastoral landscapes are different among States. In Minnesota, open or wooded pastures are used from April to October for cattle and calves, and open pastures are mostly used for sheep and lambs. During winter, they are in or near farm buildings. Turkey flocks are taken outside in June up to October, generally in fenced enclosures[50]. In the NRM, the landscape is mostly temperate steppe, with farm ranching with horses [54]. Cattle of the same livestock owner generally graze in different open pastures during different times of the year, which can be fenced [55]. The grazing period can start in March, followed by calving birth, and ends around October [56].

For all States mentioned earlier, cattle is the most common livestock concerned by verified complaints for wolf damages, but it is also the livestock with the lowest number of dead animals involved per attack (1.2 for cattle, 4.4 for sheep and 53.5 for turkeys in Minnesota [50], wolf attacks being three times deadlier for sheep in the NRM [54]).

In the NRM, the number of verified depredated cattle and sheep increased up to 2006-2013 depending on the state. The maximum number of depredated livestock ranged from 96 (Idaho, 2008) to 123 (Wyoming, 2006) for sheep, and from 195 (Wyoming, 2009) to 413 (Idaho, 2013) for sheep. Since 2009, the depredation tendency is mainly negative (except for sheep in Idaho) [57]. This is consistent with the wolf recovery from the 90s to 2011, where the population peaked (~ 600 for Montana, ~ 1 000 for Wyoming, ~ 1 700 for Idaho), and the stabilisation that followed [57].

In Michigan, the verified depredations for all livestock annually increased between 4 to 37 between 1999 and 2011, consistently with wolf recovery in the State (~ 15 in 1999, 55 in 2011), but decreased to 5 up to 2015 despite the wolf stabilisation between 60-70 individuals [52]. The wolf's expansion in Minnesota, from ~ 1 200 individuals to ~ 2 400 individuals, explained the rise in the number of verified depredations up to 1998 with around a hundred of verified claims [58]. Since then, the claims are fluctuating around this number and the wolf population stabilised [59, 60].

Southern Europe

Sheep and goat farming is very common in South of Europe, for example in Italy, North of Portugal and Greece[7], in addition to cattle farming in Italy and Portugal [61–63]. Traditionally, the pastoral practices involved extensive pastoral grazing. Flocks are small, less than 70 goats and 40 sheep per flock on average in Greece, and traditionally grazing is unfenced [62], such as in northern Portugal [61]. In Greece and in Italy, livestock is grazed within coastal areas in autumn, and is moved to mountains from late spring (in mainland for Greece, in the Apennines or in the Alps for Italy) where it spends the whole summer [62, 63]. This process is called *transhumance*. However, this practice tends to decrease with time, with the intensification of livestock production in both countries. The number of sheep and goats is not decreasing in Greece, but the livestock is using less pastures, notably those at high altitude, and is reared in

[53]: Agriculture (2021), *2020 State Agricultural Overview*

[54]: Muhly et al. (2009), 'Livestock Depredation by Wolves and the Ranching Economy in the Northwestern U.S.'

[55]: Bradley et al. (2005), 'Assessing Factors Related to Wolf Depredation of Cattle in Fenced Pastures in Montana and Idaho'

[56]: Musiani et al. (2005), 'Seasonality and Reoccurrence of Depredation and Wolf Control in Western North America'

[57]: Service et al. (2016), *Northern Rocky Mountain Wolf Recovery Program 2015 Interagency Annual Report Summary*

[58]: Harper et al. (2005), 'Causes of Wolf Depredation Increase in Minnesota from 1979-1998'

[59]: Place (2020), *Wolf-Livestock Conflict Prevention Grants. Outcomes and Impacts on Livestock Compensation Claims. FY 2017 – Present*

[60]: Natural Resources (2019), *Monitoring Minnesota's Wolf Population*

7: 8.75M of sheep, 5.3M of goats in 2000 in Greece

[61]: Pimenta et al. (2017), 'Wolf Predation on Cattle in Portugal: Assessing the Effects of Husbandry Systems'

[62]: Hadjigeorgiou (2011), 'Past, Present and Future of Pastoralism in Greece'

[63]: Pardini et al. (2011), 'Agro-Silvo-Pastoral Systems in Italy: Integration and Diversification'

sheds instead where forage is brought from other places [62, 63]. In northern Portugal, farms increased their livestock number, and part of them now use a semi-confined grazing, in pastures close to the farm, generally fenced, or were kept in sheds [61].

In Greece, depredations were mainly reported for sheep and goats compared to cattle [64], and the mean number of annual depredation events attributed to wolves was 2 198 (sd = 604) attacks for the period 2006-2012 [65].

[64]: Iliopoulos et al. (2009), 'Wolf Depredation on Livestock in Central Greece'

[65]: Petridou et al. (2019), 'Wolf Diet and Livestock Selection in Central Greece'

In Portugal, wolf attacks on cattle represented around 28% of the annual number of attacks on livestock [61]. Wolf depredation increased in the country at the beginning of the century, despite the likely stable wolf population and the increase in wild prey populations. In 2012–2013, a total of 2 725 attacks for all livestock was totalled. This amount involved 919 cattle, which is higher than any recorded annual amounts of depredated cattle in the USA. This could result from the presence of livestock in pastures almost all year round [61].

In Spain, the reported livestock lost to wolf depredation totalled 6818 in 1988, sheep representing 76% of the total, horses or donkeys 17.5% and cattle only 6.5%. At that time, most depredations occurred in mountainous area, though only inhabiting ~ 20% of the wolf population, and the phenomenon was thought to be due to the unprotected free-ranging system predominant in that area [66]. For the sole region of Asturias in Spain, partly covering mountainous area, an average of 2 951 livestock per year was officially killed by wolves from 2003 to 2010 [67].

[66]: Blanco et al. (1992), 'Distribution, Status and Conservation Problems of the Wolf Canis Lupus in Spain'

[67]: Fernández-Gil et al. (2016), 'Conflict Misleads Large Carnivore Management and Conservation'

In the Italian Alps, the depredations for all livestock are increasing[8]. A total of 630 depredations have been reported in 2019, although the identity of the most reported killed livestock was different according to the area: in the West, alongside the French border, sheep ranked first, when in the East, it was cattle[9]. Further South, in the province of Arezzo during 1998-2001, sheep and goat were the most abundant livestock amongst the reported depredations, which totalled 464 events for 1 462 dead livestock heads[10] [68]. There is no available national dataset of wolf depredation in Italy more recent than 1995 [69]. It is illegal to kill wolf in Italy, even for livestock protection, but the level of human-caused mortality is estimated at 15-20% of the total population [70].

8: following the wolf's recolonisation of the area

9: Francesca Marucco, at the Life WolfAlps web-conference, accessible here

10: No distinction was made between wolf and dog attacks however.

[68]: Gazzola et al. (2008), 'Livestock Damage and Wolf Presence'

[69]: Boitani et al. (2010), 'Ex-Post Compensation Payments for Wolf Predation on Livestock in Italy: A Tool for Conservation?'

[70]: Ciucci (2015), 'All's Well That Ends Well? Wolf Recovery and Conservation in Italy'

France

In France, along with the wolf recolonisation, the number of verified livestock deaths attributed to wolf depredation is mostly increasing every year: it was lower than 1 000 up to 1998, and exceeded 12 000 in 2019 [71]. The number of depredation events follows the same trend, reaching 3 645 reported and verified events in 2019 (~ a ratio of 3.3 dead livestock per attack)[11]. Among the reported and verified depredated livestock, sheep are by far the type of livestock the most successfully attacked by wolves, accounting for 90% of dead livestock reported for wolf damages. The positive trend in the number of depredation of sheep is not linked to the increase in the sheep production, which is currently mostly decreasing in France, including in the French Alps area [71].

[71]: Meuret et al. (2021), 'Missing Shots: Has the Possibility of Shooting Wolves Been Lacking for 20 Years in France's Livestock Protection Measures?'

11: Data from French Administration DREAL Auvergne-Rhône-Alpes

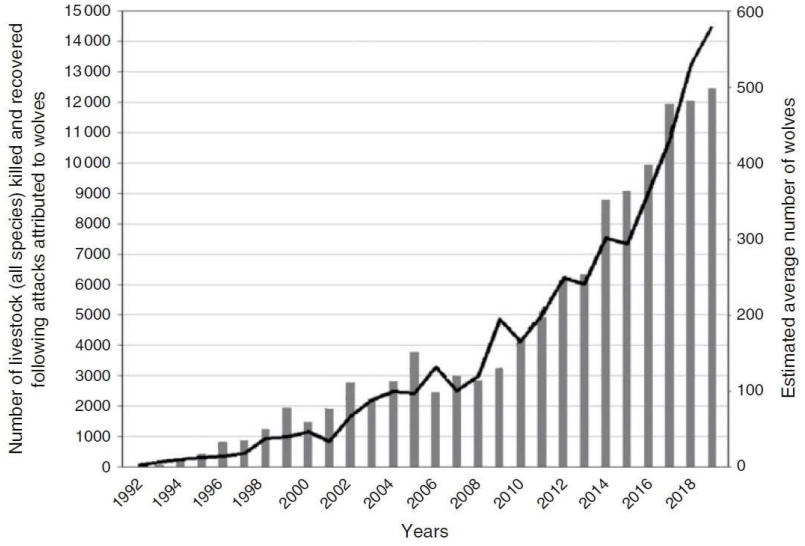


Figure 0.5: Annual number of verified livestock deaths attributed to wolf depredation (bars) and annual estimated number of wolves in France (line). Credits: Adapted from Meuret *et al.*, 2021 [71]

When the wolf started to recolonise France, depredated sheep were found in the pastures of high altitude in the Alps. These pastures are mostly used in summer for *transhumance*. As in Greece or Italy, this practice consists in moving flocks from pastures at low altitude to pastures at high altitude at the end of spring, in order to ensure regeneration of grass at low altitude and optimal grazing of flocks at high altitude during summer[12]. An opposite transhumance also exists, at lower rates, where flocks resident in mountains spend winter in hills or in plains, at low altitude where the climate is softer (Figure 0.6). The duration of grazing of flocks is therefore uneven among the pastures: pastures at high altitudes are essentially used during summer, when those at low altitude are grazed over a longer period of time. During *transhumance*, flocks of different livestock owners can be grouped together, to limit the cost of transport and herding. Sheep are the most represented livestock concerned by *transhumance*.

12: More information can be found in French on the CERPAM website

The wolf expansion in the French Alps resulted in an expansion of depredations to pastures of lower altitude. Today, pastures located in Piedmont plains or hills between the Alps and the Mediterranean sea are heavily depredated by wolves, primarily because they welcome grazing flocks almost all year round. Depredations also extended to other regions of France, in the Pyrenees (from 2005), the Jura (from 2007), the Massif Central (from 2008) and the Vosges (from 2011) [72]. However, the levels are still far lower than the ones in the Alps, mainly because density of wolves outside the Alps is very low. However, because flock division into subgroups is common in the Massif Central and in the Vosges, flocks are particularly vulnerable to wolf depredation in these areas [72].

[72]: Rossi et al. (2012), *Les moyens de protection des troupeaux domestiques contre le loup dans les nouveaux contextes de prédation*

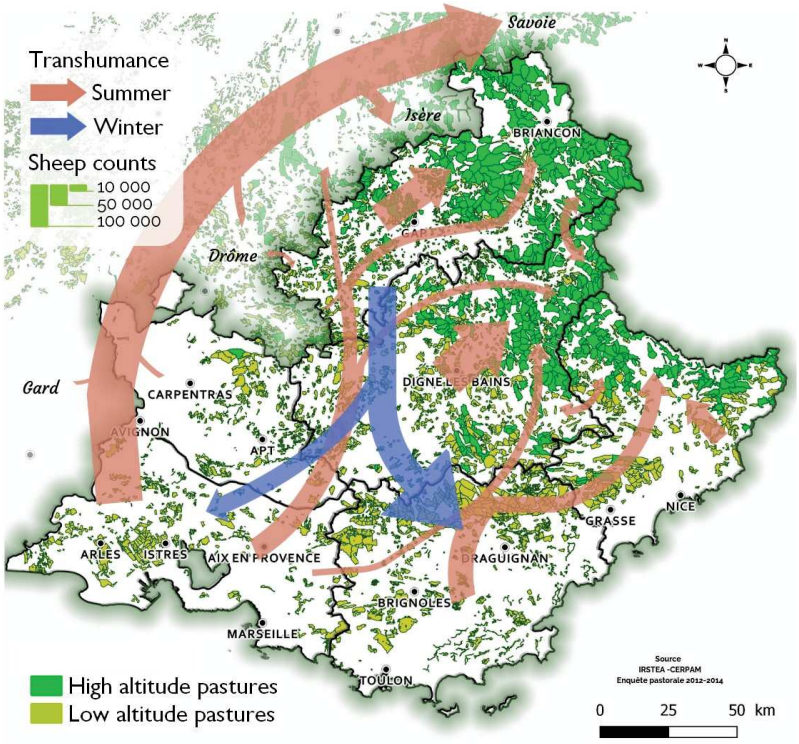


Figure 0.6: The summer and winter migrations of sheep in Provence and in the Alps, with a focus on the Provence-Alpes-Côtes-d'Azur region. Credits: CERPAM (translated into English, original map found on the CERPAM website)

The tools of the management of depredation

In France and elsewhere, to mitigate the conflict linked to depredations, three types of management tools were or are used alone or simultaneously:

1. Compensations
2. Non-lethal protective measures
3. Lethal measures

Compensations

General definition

Compensations are the financial reimbursement of all or part of the costs linked to depredations to farmers. They are not intended to stop or reduce depredations, but to increase tolerance of humans regarding depredations [73], and therefore regarding wolves.

Compensations for carnivore damages can be publicly funded, as it is generally the case in Europe [74] and in certain states of the USA (*e.g.* Minnesota). There are also other forms, like insurances or compensations provided by private funds, as the fund of '*Defenders of Wildlife*' in the US Northern Rockies area [75].

Limits of compensations

The main problem with compensations is that they are generally not equivalent to the whole set of costs linked to depredations. First, the

[73]: van Eeden et al. (2021), 'Public Willingness to Pay for Gray Wolf Conservation That Could Support a Rancher-Led Wolf-Livestock Coexistence Program'

[74]: Fourli (1999), *LIFE: Compensation for Damage Caused by Bears and Wolves in the European Union*

[75]: Dickman et al. (2011), 'A Review of Financial Instruments to Pay for Predator Conservation and Encourage Human–Carnivore Coexistence'

lost livestock are not always paid at the market value [75]. Second, there are negative side effects of depredation on the livestock production, as repeated attacks can produce stress and abortion to livestock, which are hard to evaluate. Finally, the financial compensations cannot compensate for non-financial costs, especially the stress or emotion caused to shepherds or livestock owners. Procedures for compensations can also be an additional task for farmers or marked by administrative slowness [54] [76].

[76]: Montag (2003), 'Compensation and Predator Conservation: Limitations of Compensation'

There are also certain concerns amongst conservationists that compensations might make things worse [76]. Compensation programs might increase blame towards the species only because it is the only species for which the depredations are compensated, whereas other species could be responsible (dogs or coyotes *Canis latrans* in the USA). It might also reduce the implementation of protective measures, also potentially because in some cases, compensated depredations might be more profitable than market sales [74].

Application of compensations in France

In France, the compensation scheme is driven at the State level and is funded by the French Ministry of Ecology. Each claim is controlled and checked in the field by an accredited governmental agent from the Office Français de la Biodiversité (OFB) who used a standardized protocol. Since 2018, the possibility for farmers to declare depredations without being controlled has been extended but is still under conditions. Declarations without control can only concern attacks of less than 5 sheep or goats, and only if a previous depredation claim was controlled by an accredited governmental agent [77, 78].

[77]: MTES et al. (2018), *Plan National d'Actions 2018-2023 sur le loup et les activités d'élevage*
[78]: Auvergne-Rhône-Alpes (2019), *InfoLoup. Indemnisation des dommages aux troupeaux. Numéro spécial Juillet 2019.*

Up to 2019, France compensated for any killed farmed animal for which wolf responsibility could not be discarded, regardless of protective measures. Since 2020, the implementation of protective measures is compulsory to receive compensations from the State in specific cases [79]. First, the obligation takes place only for compensations requested after two successful attacks for which wolf responsibility could not be discarded (regardless of the number of dead or wounded livestock). Second, the obligation depends on the management zone of the pasture. There are four management zones or '*cercles*' which are defined according to the number of successful attacks for which wolf responsibility could not be discarded, always regardless of the number of dead or wounded livestock (Figure 0.7) [80]. The obligation for a flock to be protected for compensation is restricted to flocks grazing within pastures of *cercle 0* or *cercle 1*.

[79]: MTES (2019), *Décret No 2019-722 Du 9 Juillet 2019 Relatif à l'indemnisation Des Dommages Causés Aux Troupeaux Domestiques Par Le Loup, l'ours et Le Lynx*

[80]: MAA (2021), *Mesures de « protection des troupeaux contre la prédation » mises en œuvre dans le cadre du règlement (UE) n°1305/2013 du Parlement et du Conseil du 17 décembre 2013 relatif au soutien au développement rural par le Fonds européen agricole pour le développement rural (Feader) en s'adossant sur les articles 20 « Service de base et rénovation des villages dans les zones rurales » (sous mesure 07.06) et 28 « mesure agroenvironnementale et climatique » (sous mesure 10.)*

The *cercles* are currently defined as followed, along with a fifth additional management zone:

1. The *cercle 0* (or *depredation hotspots*) encompasses the municipalities with a mean of at least 15 attacks over the last three years, and all the adjacent municipalities.
2. The *cercle 1* encompasses the municipalities not fulfilling the conditions for *cercle 0*, but where at least one successful attack has been verified for each of the last two years, or which have been in *cercle 1* the previous year and where at least one presence sign of

wolves has been attested by the OFB the last two years. All adjacent municipalities to those in *cercle 1* are also in *cercle 1*

3. The *cercle 2* encompasses the municipalities not fulfilling the conditions for *cercle 0* and *cercle 1*, but where at least one attack has been verified over the last three years, and all the adjacent municipalities.
4. The *cercle 3* encompasses the municipalities not fulfilling the previous conditions but within the departments where municipalities from other cercles are found, and all the municipalities of the adjacent departments.
5. The '*hardly protectable zones*' encompasses around 300 municipalities essentially from the Massif Central where the protective measures are considered economically and practically difficult to be implemented (due to the division of flocks into subgroups). They have the same rights as municipalities from *cercle 2*, but specific rights for culling that we will see in section *Application of lethal measures in France*.

The costs covered by compensation are...

(1) All livestock deaths for which wolf responsibility cannot be discarded,
(2) The loss of disappeared animals, up to the amount of the disappearances if proofs can be made, or up to 20% of the compensation for dead livestock if not,
(3) The veterinary costs for the wounded livestock (in the limits of its reimbursement if it would have been found dead)
(4) The indirect causes (stress or abortion) which may reduce the productivity, scaled accordingly to the size of the flock,
(5) The damaged material such as broken fences.

The compensations paid for wolf damages by the Ministry of Ecology has been increasing every year and totalled €3.96M in 2020 [49].

Non-lethal protective measures

General definition

Non-lethal protective measures are a large set of management tools which do not involve the death of wolves [81]. They are not only applied in the context of wolf depredation, but can be applied for other large predators too [82]. They have the aim to reduce the attempts of depredation or to reduce the success rate of the attempts.

They can be classified into four classes [83]:

- **Deterrents**. They are aimed to annihilate the predation behaviour of predators on domestic prey by creating aversion, through repellent or behaviour conditioning for instance [84]. A PhD thesis is currently ongoing to test the effectiveness of behaviour conditioning on wolf depredation behaviour in France (Matthieu Chastel, University of Antwerp).
- **Non lethal predator removal**. This method is aimed to locally reduce the abundance of the predator. It consists in the translocation of predators from areas where conflict occurs but without killing them (*e.g.* [85]), or the contraception of part of the predator population (*e.g.* [85, 86]).
- **Indirect management of land or prey**. This method consists in zoning pastoral grazing areas and wolf areas. This is the strategy used in Scandinavia where the grey wolf is confined into a conservation area in Sweden [42], and is legally hunted in the reindeer rearing area in Norway and Finland [41, 42]. Indirect management can also consists in promoting the abundance of wild preys to reduce the reliance of the predators on livestock, as suggested in [87].
- **Preventive husbandry**. It encompasses a large variety of husbandry techniques, some old, other new, which consists in disrupting the attempts of depredation. For example the coloured flags called fladry, traditionally used to direct wolves during wolf hunting in eastern Europe and Russia, has been recently used to encircle livestock and acts as a visual barrier [88] [89]. Its efficiency decreases

[81]: Bangs et al. (2006), 'Non-Lethal and Lethal Tools to Manage Wolf-Livestock Conflict in the Northwestern United States'

[82]: Eklund et al. (2017), 'Limited Evidence on the Effectiveness of Interventions to Reduce Livestock Predation by Large Carnivores'

[83]: Miller et al. (2016), 'Livestock Losses and Hotspots of Attack from Tigers and Leopards in Kanha Tiger Reserve, Central India'

[84]: Tobajas et al. (2019), 'Selection of New Chemicals to Be Used in Conditioned Aversion for Non-Lethal Predation Control'

[85]: Schmidt et al. (2017), 'Effects of Control on the Dynamics of an Adjacent Protected Wolf Population in Interior Alaska'

[86]: Haight et al. (1997), 'Computer Simulation of Vasectomy for Wolf Control'

[87]: Linnell et al. (2012), 'Mitigation Methods for Conflicts Associated with Carnivore Depredation on Livestock'

[88]: Iliopoulos et al. (2019), 'Tools for Co-Existence: Fladry Corrals Efficiently Repel Wild Wolves (Canis Lupus) from Experimental Baiting Sites'

[89]: Musiani et al. (2003), 'Wolf Depredation Trends and the Use of Fladry Barriers to Protect Livestock in Western North America'

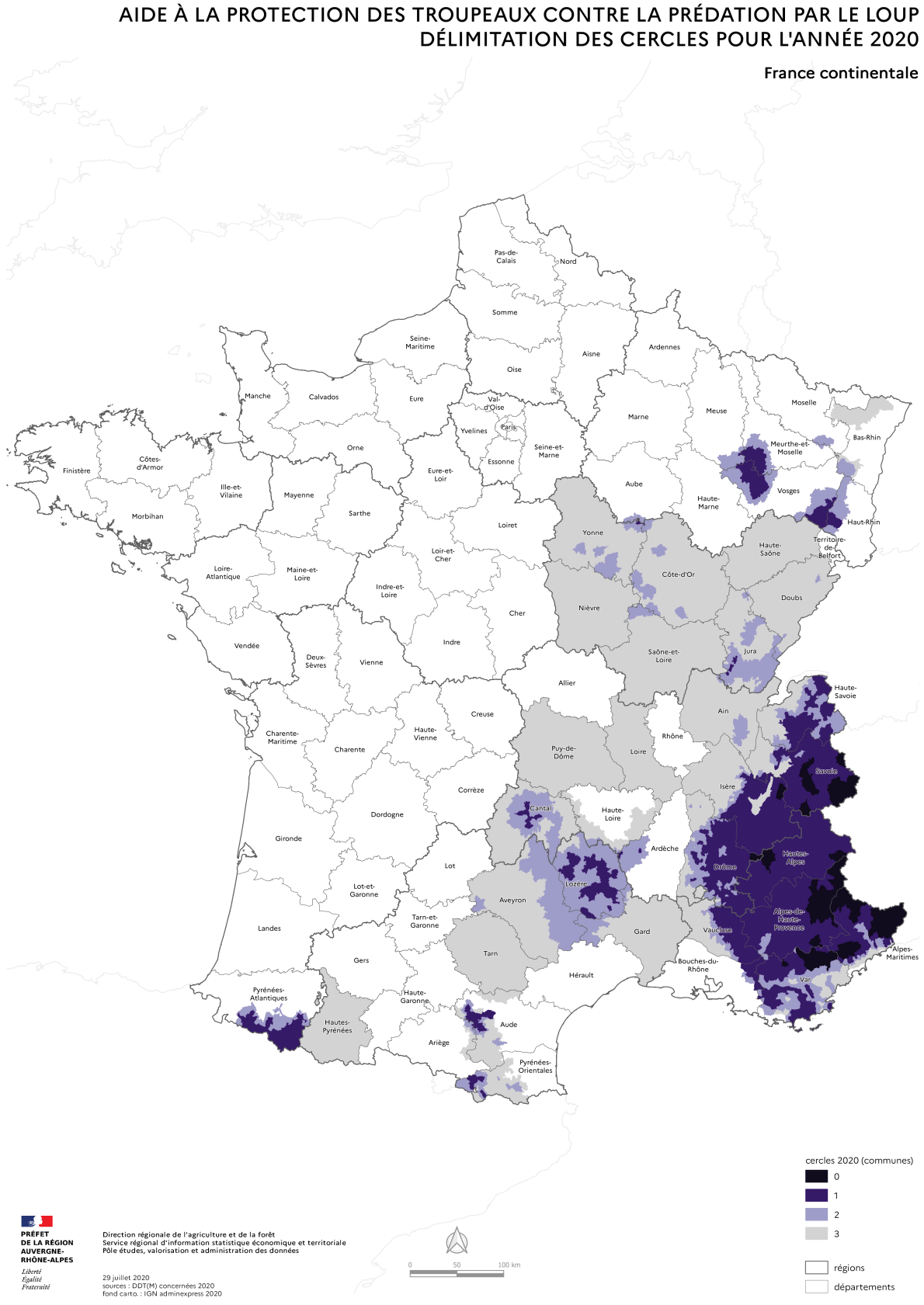


Figure 0.7: The four zones or *'cercles'* used for management of depredations in France. The delimitation of municipalities in the last additional zone *'hardly protectedly zones'* is not shown here. Credits: Direction Régionale de l'Agriculture et de la Forêt d'Auvergne-Rhône-Alpes.

with time [82] and was dependent on the attractiveness of what is inside the fladry barrier [88]. Amongst the oldest husbandry protective techniques, you can find **fences, livestock guarding dogs and shepherds**, used separately or combined.

The cost of implementation of protective measures should also not exceed the expected cost of depredation [82] [90], yet these measures can be costly [81]. Protective measure cost involves the investment of material but also the running costs [82], as salaries for shepherds, veterinary costs for dogs, additional time spent to manage the measures, etc... In most countries from Europe and most states in the USA facing wolf-livestock conflicts, public subsidies are provided to farmers to make the implementation of protective measures such as fences and dogs less costly and economically viable [91].

[90]: Shivik (2006), 'Tools for the Edge: What's New for Conserving Carnivores'

[91]: Karlsson et al. (2011), 'Subsidized Fencing of Livestock as a Means of Increasing Tolerance for Wolves'

Shepherds, guarding dogs and fences

Flock watching by shepherds or guarding dogs is an old husbandry technique [92], but today new challenges for their implementation appear. Shepherds can be hard to find for farmers, and to keep on the long term because the activity involves hard work for low wages, including in the USA [81]. In France, there are currently more demand from farmers to hire shepherds than available shepherds, even if the number of shepherds is progressively increasing. The majority of shepherds in France have temporary contracts [93] and their particular working schedules are difficult to combine with the legal framework. This makes their official working status very precarious, and therefore the activity less attractive[13].

After the near-disappearances of the use of shepherds and livestock guarding dogs with the extinction of wolves in France, there is a need to structure the national shepherd network and breeding sector of livestock guarding dogs [77]. Shepherds have now to deal with more frequent outdoor activities such as hiking or biking, sometimes interfering with husbandry, especially in mountains[13] [77]. Communication is therefore required to inform people on how to respond to livestock guarding dogs, in order to prevent accidents.

Be aware of the dog

Livestock guarding dogs should not be confused with herding dogs which helps shepherds to move flocks (*e.g. border collies*). The livestock guarding dogs are bigger and have been selected to specifically defend flocks by repelling intruders (*e.g.* Pyrenean Mountain Dog or '*patou*', Figure 0.8) [92].

[92]: Rigg (2001), *Livestock Guarding Dogs: Their Current Use World Wide*

[93]: Bonnet et al. (2020), *Une vaste enquête sur le métier, les profils et les attentes des bergères, bergers et vachers salariés des Alpes*

13: Webconference '*Travail salarié en milieu pastoral : quelle attractivité, vivabilité et perennité pour les métiers ?*', Association Française de Pastoralisme, Institut de l'élevage, INRAE, 24th November 2021



Figure 0.8: A livestock guarding dog, from the Pyrenean Mountain breed (*patou*), in a flock of sheep surrounded by mobile fences, in France. Credits: Bertrand Muffat-Joly.

Concerning fences, they can be of two main types: permanent or mobile. Permanent fencing or enclosure are especially adapted to grazing in pastures used all year round by livestock, in flat and accessible areas, near farms, as in the semi-confined system in Portugal [61]. However, in the context of *transhumance*, permanent fencing is not adapted, as the pastures are only temporarily used, in often remote and steep areas far from farm buildings [88]. In addition, in France, pastures used for *transhumance* can be rented and not owned (C. Duchamp, OFB, *pers. com.*), making the settlement of permanent fencing economically less viable for these pastures. This is why in this specific context, mobile fences that can be easily moved from one pasture to the other can be used [87] (Figure 0.8).

However, it has been showed that wolves can learn to bypass or jump above fences, even if they are electrified ([12], see more details in Chapter 2). Fences can also exacerbate depredations because when a predator succeeds to penetrate inside an enclosure, it generally triggers what is called '*surplus killing*', a phenomenon where a predator kills a large number of prey during the same attack [64].

Actually, permanent or mobile fences facilitate the surveillance of flocks by dogs or humans rather than preventing predators to enter [94]. This is why fences can be more efficient when combined to livestock guarding dogs or humans. Livestock guarding dogs and shepherds have proven efficient in Greece to reduce the number of killed livestock per attack compared to unguarded flocks even if flocks were enclosed [64]. For dogs, their efficiency depended on the number of dogs in relation to flock size [64].

[94]: Rigg et al. (2011), 'Mitigating Carnivore–Livestock Conflict in Europe: Lessons from Slovakia'

Subsidies of non-lethal measures in France

In France, public subsidies originate from the Ministry of Agriculture and from the European Agricultural Fund for Rural Development [77]. Subsidies can be allocated for the costs linked to the use of **shepherding**, **livestock guarding dogs** and **fences** [80] [95]. The subsidies for each type of measure correspond to 80% of its material investments, and 80% of its running costs. In addition, a flock vulnerability analysis and a technical support for the implementation of protective measures can also be subsidised at 100%.

[95]: l'Alimentation (2019), *Arrêté Du 28 Novembre 2019 Relatif à l'opération de Protection de l'environnement Dans Les Espaces Ruraux Portant Sur La Protection Des Troupeaux Contre La Prédation*

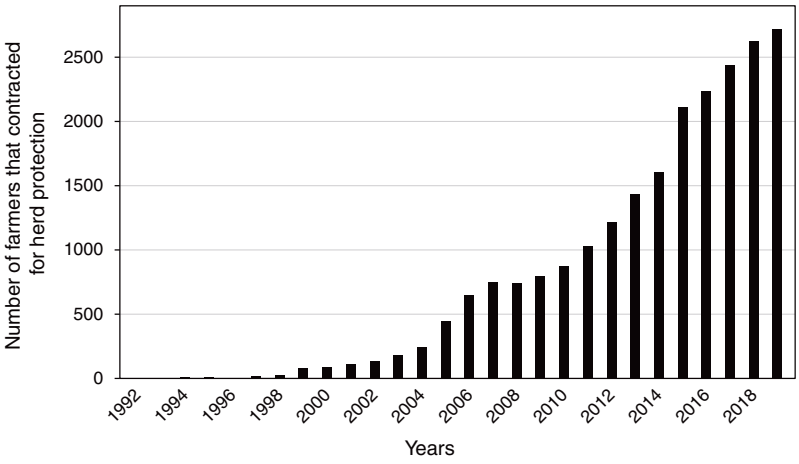
Only flocks of at least 25 sheep or goats are eligible to protective measures subsidies. The eligibility of each farmer to receive the subsidy for each of the 5 different non lethal protective measures is depending on the grazing time of its flock and the location of its flock within the management zones called '*cercles*' that we have seen in section *Compensations*. Allocation of subsidies is then organised according to 3 groups:

1. The flock is grazing for at least 30 days during the year in *cercle 0* and/or *cercle 1*. The farmer is eligible for the 3 protective measures, the vulnerability analysis and the technical support.To receive subsidies, the subscription for at least two of the three protective measures is compulsory.

Subsidies cap

All subsidies are capped. The cap of subsidies increases with flock size, from group 1 to 3, and is higher for the *transhumant* husbandry system than for systems where flocks mostly graze inside permanent enclosures. The subsidy for shepherding is not capped for flocks grazing in *cercle 0* for at least 90 days, these areas being considered as depredation hotspots. The subsidy is risen to 100% for flocks located within the core of national parks.

2. The flock is not fulfilling the previous condition, but is grazing for at least 30 days during the year in *cercle 0*, *cercle 1* and *cercle 2*. The farmer is not eligible to the subsidies for shepherding and flock vulnerability analysis.
3. The flock is not fulfilling the two previous conditions, but is grazing for at least 90 days during the year in *cercle 0*, *cercle 1*, *cercle 2* and *cercle 3*. The farmer is only eligible to subsidies for livestock guarding dogs and technical support.



The trend of subsidies for non-lethal protection

Along with the wolf recolonisation and the increase in the number of depredations, the number of livestock owners who subscribe for non-lethal protective measures subsidies is increasing every year in France (Figure 0.9, [71]). In 2020, these subsidies in the context of wolf depredations totalled €28.63M [49].

Figure 0.9: Number of contracts for subsidies for non-lethal protective measures against wolf depredation in France. Credits: Meuret *et al.*, 2021 [71]

Lethal measures

General definition

Lethal measures are also a set of management tools, although less varied than the set of non-lethal protective measures. As the name suggests it, these measures involve the death of wolves, and have also been applied to other large predators in the context of depredation. They have the aim to reduce the occurrences of encounters between predators and livestock or to remove individuals inclined to depredation. There are different types of lethal removal which depends on 4 main parameters:

- **Type of removal tool**. To kill wolves, several tools have been applied, separately or simultaneously:
  - trapping [52] [96–98],
  - poisoning [99],
  - aerial shooting [96, 98],
  - ground shooting [96, 98].
- **Type of removers**. Removal can be applied by (exclusively or combined) [96, 98] [100]:
  - governmental agents,
  - hunters,
  - livestock owners.
- **Removal intensity**. One or several wolves can be killed at a time. In the USA, the removal of entire packs has also been applied [96].
- **Removal selectivity**. There are different level of selectivity.

[96]: Bradley et al. (2015), 'Effects of Wolf Removal on Livestock Depredation Recurrence and Wolf Recovery in Montana, Idaho, and Wyoming'
[97]: Harper et al. (2008), 'Effectiveness of Lethal, Directed Wolf-Depredation Control in Minnesota'
[98]: DeCesare et al. (2018), 'Wolf-Livestock Conflict and the Effects of Wolf Management'
[99]: Bjorge et al. (1985), 'Evaluation of Wolf Control to Reduce Cattle Predation in Alberta'
[100]: Wielgus et al. (2014), 'Effects of Wolf Mortality on Livestock Depredations'

- Removal can be aimed to target the '*problem individuals*' which are individuals which kill more livestock than others. The practical identification of such individuals can however be challenging [101].
- Removal is semi-targeted, with the aim to locally reduce the predator abundance in specific areas. For example in Finland, wolves are hunted in the reindeer herding areas in the North of the country [41].
- Removal is not targeted, and have the aim to reduce the whole predator population at a large scale [101].

[101]: Linnell et al. (1999), 'Large Carnivores That Kill Livestock: Do "Problem Individuals" Really Exist?'

Legal context in Europe

As said in section *...to full protection..*, *Canis lupus* is currently a protected species across all Europe. How is it possible to apply lethal measures in this context? Derogations to the strict status of protection of the species listed in Annex II of the Bern Convention (1979) or in Annex IV of the Habitats Directive (1992) are possible under certain conditions according to Article 9 or Article 12, respectively. Article 12 of the Habitats Directive (1992) stipulates:

> '*Provided that* ***there is no satisfactory alternative*** *and* ***the derogation is not detrimental*** *to the maintenance of the populations of the species concerned at a* ***favourable conservation status*** *in their natural range, Member States may derogate from the provisions of Articles 12*[14]*, 13, 14 and 15 (a) and (b): [...]* ***to prevent serious damage****, in particular to crops,* ***livestock****, forests, fisheries and water and other types of property [...].*'

14: Article 12 attributes '*strict protection for the animal species listed in Annex IV*' which contains the grey wolf

Thus, the Member States of the Bern Convention or the Habitats Directive can call Article 9 or Article 12, respectively, to authorise lethal removals for livestock protection. In the case of depredations, the '*satisfactory alternative*' mentioned in both articles refers to the implementation of compensations and non-lethal protective measures if possible. In other words, if depredation persists despite the use of non-lethal mitigation measures if applicable, and if livestock damage is high, derogations to the strict protection of wolves can be authorised by the Member States (as France).

In France, the application of lethal measures to manage wolf depredations is made under Article 16 of the Directive Habitats, such as Slovenia [102] and Sweden [103]. Not all European countries have nevertheless call this article to allow derogative culling to protect livestock. It is the case of Italy [102], where no derogation had been made at least up to 2016. However, the Italian wolf management plan seeks to allow such derogations with a ceiling [104], and the Italian wolf population is already subjected to an intense poaching '*tacitly accepted by public authorities*' [70].

[102]: Schnidrig et al. (2016), *Wolf in the Alps: Recommendations for an Internationally Coordinated Management*

[103]: Commission (2011), *Commission Urges Sweden to Respect Nature Legislation in Protecting Endangered Wolves*

[104]: Boitani (2016), 'Wolves in Italy: The New Wolf Management and Conservation Plan in 2016'

In some countries, as Greece, Spain and Finland, the grey wolf is listed in Annex IV of the Directive Habitats only for one part of the country, and under Annex V for the other part [105], which permits hunting if the conservation status of the species is ensured [46]. In Finland, the area under Annex V concerns the northern part of the country, where the reindeer husbandry area is located [46]. In Spain, wolf was considered a game species in the North West of the country [106]. The Spanish

[105]: Trouwborst et al. (2019), 'Killing Wolves Legally: Exploring the Scope for Lethal Wolf Management under European Nature Conservation Law'

[106]: Taussig de Bodonia (2019), 'Coexistence with Large Carnivores in the North West of Spain'

government has however announced its intention to forbid wolf hunting over the whole country [107].

Even under Annex IV, wolf hunting has been authorised. In Sweden, a wolf hunting season has been repeatedly authorised by the government since 2009 in order to maintain the wolf population under an arbitrary ceiling of 210 wolves and within a management area [103] [108]. This led Sweden to be in conflict with the European Commission in 2011, as the Swedish wolf population is under Annex IV of the Habitats Directive and that the conditions mentioned in Article 12 were not respected for allowing wolf hunting [103]. A similar management is in place in Norway, which shares its wolf population with Sweden, but has only ratified the Bern Convention, as it is not part of the European Union [109].

[107]: Transición Ecológica y el Reto Demográficoobierno de Espana (2020), *El borrador de la Estrategia para la Conservación y Gestión del Lobo propone su inclusión en el listado de Protección Especial icono barra herramientas*

[108]: Cinque (2015), 'Collaborative Management in Wolf Licensed Hunting: The Dilemmas of Public Managers in Moving Collaboration Forward'

[109]: Trouwborst et al. (2017), 'Norway's Wolf Policy and the Bern Convention on European Wildlife: Avoiding the "Manifestly Absurd"'

Quota for lethal measures in France

Lethal measures to protect flocks from wolf depredation are legally applied in France since 2004, where the first National Wolf Management Plan (NWMP) came into effect under the auspices of the Ministry of Ecology and the Ministry of Agriculture [110]. The French State attempts to limit the increase of depredations since the recolonisation of the grey wolves in the country in the 1990s, while ensuring that its measures are not '*detrimental to the maintenance of the populations of the species concerned at a favourable conservation status*'. In the Directive Habitats, the favourable status is defined as a stable or growing population whose habitat is '*neither being reduced nor is likely to be reduced for the foreseeable future*'.

[110]: MTES et al. (2004), *Plan d'Action sur le loup 2004-2008*

The French State opted in 2004 for a culling quota which sets a threshold on the number of wolves that can be culled, determined for the period running from July of year *y* to June of year *y+1* [110]. This period is chosen to have the wolf population size estimates available (see box *Réseau Loup-Lynx*). The culling quota was set at 10% of the population size, consistently with the recommendation of [111], based on predictive modelling of control strategies for a simulated population of *Canis lupus*. The annual growth being reported at 20% for 55 individuals in 2004 in the NWMP, the culling quota represented half of the annual growth. The culling quota of 10% of the population size was maintained in the next NWMP for the period 2008-2012 [112].

[111]: Chapron et al. (2003), 'Conservation and Control Strategies for the Wolf (Canis Lupus) in Western Europe Based on Demographic Models'

[112]: Duchamp et al. (2017), *Expertise collective scientifique sur la viabilité et le devenir de la population de loups en France à long terme sous la coordination ONCFS-MNHN de : Guinot-Ghestem M., Haffner P., Marboutin E., Rousset G., Savoure-Soubelet A., Siblet J.P., Trudelle L.*

In the following NWMP for the period 2013-2017 [113], the method is adapted to take into account the uncertainty about the estimation of the population size and of its growth rate. The culling quota was set at 24 wolves for 2013-2014 and 2014-2015, and increased to 36 wolves for 2015-2016 and 2016-2017. The quota had to guaranty the probability of stability or of increase of the wolf population in France was higher than the probability of decrease.

[113]: MTES et al. (2018), *État des lieux et diagnostic de la situation dans la perspective de la rédaction du futur plan national d'actions 2018-2023 sur le loup et les activités d'élevage*

In the next and current NWMP for the period 2018-2021 [77], the culling quota is set for each year from January to December[15]. The culling quota of 10% of the population size from the first two NWMP is adopted again, and can be extended to 12% only for two culling classes, the simple and reinforced livestock defence culling, that I define later [114].

15: To avoid that the culling quota overlaps two summers, when peaks of depredations happen.

[114]: MTES (2018), *Arrêté Du 19 Février 2018 Fixant Le Nombre Maximum de Spécimens de Loups (Canis Lupus) Dont La Destruction Pourra Être Autorisée Chaque Année*

Réseau Loup-Lynx

Réseau Loup-Lynx (or the Wolf-Lynx French Network) is in charge of the wolf monitoring in France, and is supervised by the OFB. It is predominantly composed by agents from different public organisms (56%[a]), the majority working for the OFB. It also involves 16% of its members from the general public, 13% of hunters, 8% of members from environmental protection associations and 2% of people from the agriculture sector (source: OFB).
All members of the network are trained to opportunistically collect presence signs all year along, such as feces, hairs, tracks or observations (notably through camera-traps, Figure 0.10). Two intensive surveys are also conducted in summer and in winter within the detected or suspected wolf territories [115]. Biological indices are analysed for genetic identification of the species and of the individual.
From the monitoring, in addition to the distribution map of temporary or permanent presence (Figure 0.4), three main metrics are produced:

- The **number and locations of wolf territories**, updated at the end of each intensive survey. The winter survey allows the estimation of the number of individuals within territories (through track monitoring), and the summer survey allows the identification of reproductive packs (through induced howling monitoring).
- The **annual number of genetically identified wolves** at the end of each winter.
- The **annual estimated size of the wolf population** at the end of each winter, based on the number of detected wolves and the application of a non-spatial open mark-recapture model [116].

[a] in 2018



Figure 0.10: Camera-trap data collected by Catherine Vuiton, member of Réseau Loup-Lynx and of the OFB, in Hérault, France. Credits: O. Grente

[116]: Cubaynes et al. (2010), 'Importance of Accounting for Detection Heterogeneity When Estimating Abundance: The Case of French Wolves'

At the end of 2018, the estimated number of wolves in France reached 500 individuals [117]. This corresponded to the number of wolves necessary to keep the risk of demographic extinction[16] lower than 10% over 100 years for a stable population according to different models [118]. This limit was used by the French authorities to define the wolf viability threshold in France [119]. Above this threshold, France considered that the wolf population was now in a favourable conservation status, and that the population growth was therefore not compulsory to ensure the conservation of the species if the population was maintained above the viability threshold.

Once the wolf population in France reached this viability threshold at the end of 2018, the culling quota has been increased to 19% on an '*experimental basis*' [120]. Despite this increase, the wolf growth rate remained positive, at of 9% at the end of 2019 and 8% at the end of 2020 [29]. This is why the experimental culling quota was formalised, and has even been extended in 2021 to 21% for the simple livestock defence culling (it remains at 19% for the other culling class) [121].

Each year, the maximum number of wolves that can be culled is updated through a decree delivered by the Ministry of Ecology, based on the culling quota and the winter estimates of the wolf population size

[117]: Office Français de la Biodiversité (2019), *Bilan hivernal de la population de loup : le seuil des 500 loups est atteint*

16: Note that to prevent genetic deficiencies of an animal population, around 2 500 – 5 000 adults would be required [112]

[118]: Chapron et al. (2012), *Demographic Viability of the Scandinavian Wolf Population*

[119]: MTES (2020), *Motif de décision de l'arrêté ministériel du 30 décembre 2019 portant expérimentation de diverses dispositions en matière de dérogations aux interdictions de destruction pouvant être accordées par les préfets concernant le loup (Canis lupus)*

[120]: MTES (2019), *Arrêté du 26 juillet 2019 portant expérimentation de diverses dispositions en matière de dérogations aux interdictions de destruction pouvant être accordées par les préfets concernant le loup (Canis lupus)*

[121]: MTE (2020), *Arrêté du 23 octobre 2020 fixant le nombre maximum de spécimens de loups (Canis lupus) dont la destruction pourra être autorisée chaque année*

provided by the OFB [121]. The conditions of application of culling are stipulated in a different decree [122].

[122]: MTE (2020), *Arrêté du 23 octobre 2020 fixant les conditions et limites dans lesquelles des dérogations aux interdictions de destruction peuvent être accordées par les préfets concernant le loup (Canis lupus)*

Parameters of culling in France:

Tool: Ground shooting.
Removers: Governmental agents, hunters and livestock owners.
Intensity: Several wolves can be culled at the same time (never with the aim to remove an entire pack).
Selectivity: Two types: (1) wolves approaching flocks only and (2) any wolf of areas with high depredation levels.

Application of lethal measures in France

The derogations for lethal measures (or '*culling*') are delivered to one or several farmers [122]. They cannot be delivered for flocks grazing within core of national parks where hunting is forbidden (such as the MNP).

Currently, most wolves culled in the context of derogative culling in France are removed by governmental agents. There are of two types:

- The *brigadiers*. They are staff members of the OFB. Their status has been created in 2015 by the Ministry of Ecology specifically for the purpose of increasing the protection of flocks against large predator depredation, notably by applying lethal shootings. Currently, there are 16 brigadiers who work at the national level, in the context of depredations by wolves but also by Eurasian lynxes (*Lynx lynx*) and by brown bears (*Ursus arctos arctos*). They are equipped with thermal cameras and thermal scope.
- The *lieutenants de louveterie* are volunteer agents named by departmental prefects. Their status originate from the status of '*louvetiers*' created under the reign of Charlemagne in the eighth century with the purpose of eradicating species considered as pests. With the disappearance of the grey wolves in the twentieth century, their missions have been broadened to the management of other species which cause damages on livestock or crops, such as wild boar (*Sus crofa*), but not to their eradication anymore. They are now enlisted in the context of wolf depredation management. The travel expenses and part of their equipment are financed by the Departmental Direction of Territories (DDT). They are progressively equipped with thermal cameras and thermal scope.

The culling is currently divided into three classes of progressive intensity in response to depredation (Table 0.2).



Figure 0.11: A *brigadier*, a governmental agent of the OFB, watching over a grazing flock of sheep, as part of the preparation of the night operation of wolf culling, in France. Credits: Bertrand Muffat-Joly.

Table 0.2: The three types of culling in 2021 in France [122].

	Simple defence culling	Reinforced defence culling	Harvest
Conditions	Implemented non-lethal protective measures	Implemented non-lethal protective measures. ≥ 3 depredations for the last 12 months.	An *'exceptional'* level of damages on several flocks protected by non-lethal measures and simple defence culling
Validity	≤ 5 years	Ongoing year	Ongoing year
Application	Only one shooter, near the flock. The shooter can be the recipient of the decree or any person mandated by this recipient. Valid hunting licence required.	Operations of generally several days supervised by *brigadiers* or by *lieutenants de louveterie*. ≤ 10 shooters, near flocks. Hunters with specific training from the OFB are authorised but without use of thermal cameras.	Operations supervised by *brigadiers* or by *lieutenants de louveterie* in a specific area, not necessarily at proximity of flocks. Hunters with specific training from OFB are authorised but without use of thermal cameras. It can also take place during a big game hunting where any hunter can participate. Limits in the number of wolves that can be culled.
Time	Any moment	Any moment during an operation	From July to December

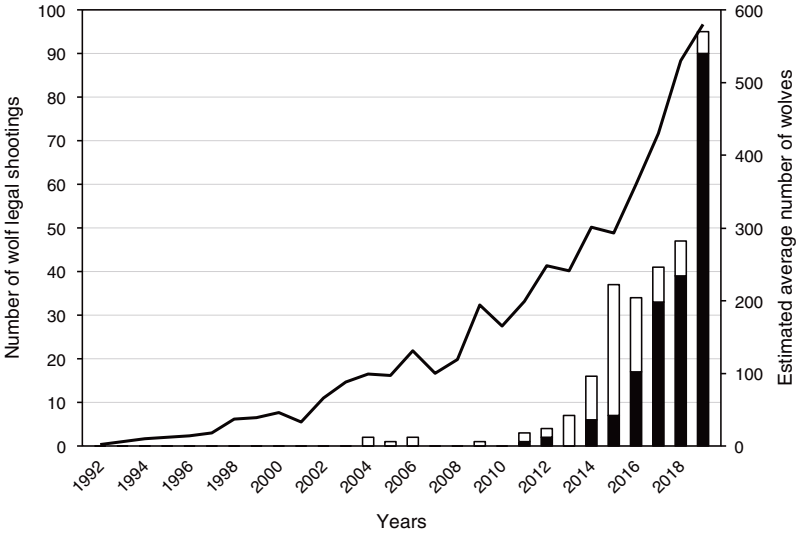


Figure 0.12: Annual number of culled wolves in France (closed bars, simple and reinforced livestock defence culling; open bars, harvesting) and annual estimated number of wolves in France, from 1992 to 2019. Credits: Meuret *et al.*, 2021 [71]

The culling trend

Along with the wolf recolonisation, the increase of depredation, and the recent extension of the culling quota, the number of legally culled wolves is increasing every year in France (Figure 0.12 [71]). In 2020, the number of legally culled wolves was 97 [49].

Controversy

Lethal measures to manage the conflicts linked to depredation is by far the most controversial of the three management tools [94] [123]. The support for wolf removal to protect livestock from depredation is generally high amongst the livestock owner community [87]. On the contrary, the support can be low for people indicating that their first interest was environmental protection, as shown in a study in Utah [123]. Thus, the first group will advocate for more wolf removals whereas the

[123]: Bruskotter et al. (2009), 'Social and Cognitive Correlates of Utah Residents' Acceptance of the Lethal Control of Wolves'

second group will advocate for less or no wolf removals (Figure 0.13) [81]. The livestock community will defend economic interests, along with needs for empowerment [87], when environmental activists will highlight ethical standards and the predator conservation [124]. Social conflicts emerge from the split between both stakeholders, and take an important place in the conservation management of large predators: '*conflicts are as much the result of conflicts between people as between people and large predators*' [125]. This is particularly exacerbated in Norway where hunters and environmental activists confront over wolf hunting, sometimes up to threats (see the documentary '*The Wolf Dividing Norway: the hunter v the environmentalist*' from the Guardian in 2020).

[124]: van Eeden et al. (2018), 'Carnivore Conservation Needs Evidence-Based Livestock Protection'

[125]: Andersen et al. (2003), *Large Predators and Human Communities in Norway. A Guide to Coexistence for the 21st Century.*

Among these two polarised groups, general public appears divided concerning the use of lethal measures for livestock protection [87]. In Slovakia, the proportions of surveyed people favourable and unfavourable to predator lethal removals in areas with depredations were equal. In Sweden and in the USA, people appeared in favour of predator control for livestock protection at 53% and 60% respectively, the other being neutral (17% and 23%) or disagreeing (30% and 16%) [126, 127]. People living in wolf areas in Sweden, or in rural or small towns in the USA, reported higher levels of acceptance of predator control than people in urban areas [126, 127]. The acceptance also depended on the type of removal tool, with low acceptance for traps or aerial shooting compared to poison or shooting in the USA [127]. In addition, the general public in Wisconsin appeared divided concerning the optimal size of wolf population in their state, the proportions being in favour of no cap or of a 100-wolves cap being equal [128]. However, the extermination of wolves from Wisconsin was not supported by any of the social groups, whether it is the group of livestock owners, of hunters or of the general public [128]. Apart from large predators, the controversy for lethal measures is also true for other species such as geese or deer which cause damages on crops in the Netherlands, with divided opinions in the urban areas, and a shift towards acceptance in rural areas [129].

[126]: Ericsson et al. (2004), 'Support for Hunting as a Means of Wolf Canis Lupus Population Control in Sweden'
[127]: Reiter et al. (1999), 'Public Attitudes toward Wildlife Damage Management and Policy'

[128]: Naughton-Treves et al. (2003), 'Paying for Tolerance: Rural Citizens' Attitudes toward Wolf Depredation and Compensation'

[129]: Sijtsma et al. (2012), 'Acceptability of Lethal Control of Wildlife That Damage Agriculture in the Netherlands'

Ecologists are as much divided as the general public regarding the use of lethal removals to reduce depredation [7]. They showed more beliefs in the effectiveness of targeted removal compared to public harvest [7, 87] [130], with however low consensus for both measures [7]. In a review about contemporary lethal control programmes, [131] concluded that '[...] *lethal control is a legitimate part of wildlife management and as such can play a*

[130]: Boitani (2000), *Action Plan for the Conservation of the Wolves (Canis Lupus) in Europe*

[131]: Treves et al. (2005), 'Evaluating Lethal Control in the Management of Human–Wildlife Conflict'



Figure 0.13: Protest march (left) for '*the right to kill wolves to defend livestock*' in Paris, France, 27th November 2014, (right) '*to denounce the wolf plan management in France, judged as elimination rather than management*' in Lyon, France, 16th January 2016. Credits: Daniel Wambach (left), Fondation Bardot (right).

role in conservation. The more difficult questions lie in who should be allowed to kill which animals and under what circumstances.' [131] suggested that highly selective removals towards problem individuals by trained agents should be preferred over public hunting for species on the brink of extinction, but that public hunting could be reintegrated to the management tools once the species has recovered.

Efficiency and effects of lethal measures

The origin of the controversy around lethal removals takes root in the uncertainty surrounding the effects of the lethal measures [124] [132–135]. Even if this uncertainty also applies for non-lethal measures [82], the controversy is higher for lethal control because of the consequences removals of individuals can have on the predator conservation [124].

So far, two competing assumptions prevail regarding the effects of lethal removal of large predators [133]. In the specific case of wolves, these assumptions take into account the social structure of the wolf population in packs:

Assumption 1 *Lethal removal is decreasing the depredation level by:*

- *Decreasing predator population size (reported in [133]),*
- *Threatening survivors and/or selecting individuals less likely to depredate [71].*

Assumption 2 *Lethal removal is increasing the depredation level by:*

- *Increasing reproduction rates by favouring multiple breeding (reported in [133]),*
- *Dislocating packs, causing isolated individuals... [52]*
- *And favouring colonisation by new individuals, naive to local wild prey [51].*

These two assumptions are contradictory about the effects of lethal removals on the depredation levels because they disagree on the effects lethal removal can have on the remaining wolves of the population (Figure 0.14).

Both assumptions are not always mutually exclusive. For example, the decrease in population size from Assumption 1 could be true, as well as the dislocation of packs. In this case, both effects could cancel one another out, and lethal removal could have no effect on the depredation levels, instead of decreasing or increasing it [133].

Scientific studies have been conducted to test these assumptions. However, to my knowledge, none have analysed simultaneously 1) the effects of lethal removals on wolf population and 2) the repercussions of these population changes on the depredation levels, based on field data. So far, studies have conducted separately their analyses for each of the axes relative to the effect of lethal removals of grey wolves (Figure 0.15). This lack of integrative studies partly explains why there is still no clear knowledge about the effect of lethal removals of wolves.

[132]: Treves et al. (2016), 'Predator Control Should Not Be a Shot in the Dark'
[133]: Treves et al. (2019), 'Predator Control Needs a Standard of Unbiased Randomized Experiments With Cross-Over Design'
[134]: Lennox et al. (2018), 'Evaluating the Efficacy of Predator Removal in a Conflict-Prone World'
[135]: Miller et al. (2016), 'Effectiveness of Contemporary Techniques for Reducing Livestock Depredations by Large Carnivores'

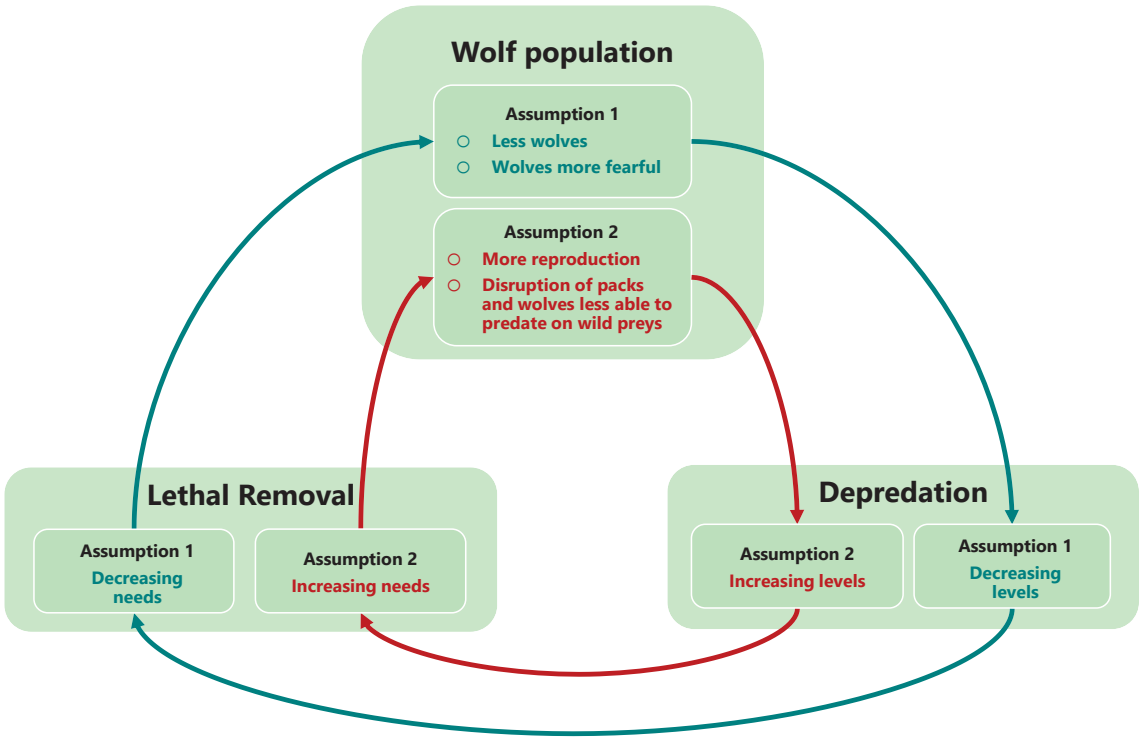


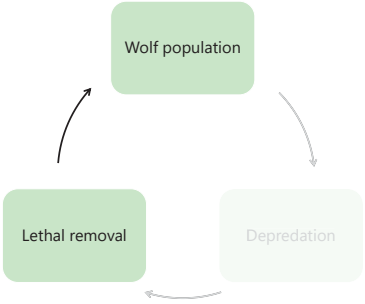
Figure 0.14: Representation of the two opposite assumptions about the effect of lethal removals when applied on wolves with the aim to reduce depredation levels. Credits: O. Grente.

Analyses of Axis III (Figure 3.1) could provide sufficient clues about the efficiency of lethal removals. Indeed, there is not an absolute need to know precisely the effect of removals on the wolf population to evaluate its effect on the depredation levels. I have identified 9 studies which included this type of analysis for the grey wolf (*e.g.* [96]). If we include studies on two other species sharing a similar social structure with grey wolves, dingos (*Dingo dingo*) and coyotes (*Canis latrans*) from the *Canidae* family, the total of studies reaches 9 (wolf) + 3 (dingo) + 3 (coyote) = 15.

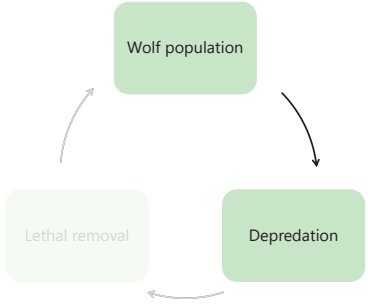
However, none of these studies was experimental[17], while **experimental studies** provide the highest strength of scientific evidence (*i.e.* inference).

17: except one on dingo (Allen *et al.*, 2014 [138]) but with proxies for predation and predator removals.

(a) Axis I: The effect of lethal removal on wolf population (*e.g.* [136])



(b) Axis II: The relationship between wolf population structure and depredation (*e.g.* [137])



(c) Axis III: The direct effect of lethal removal of wolves on the levels of depredation (*e.g.* [96])

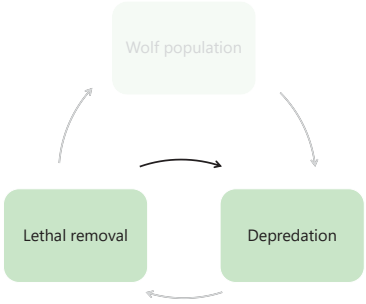


Figure 0.15: The three axes of analysis related to the study of the effect of lethal removals of grey wolves found in the scientific literature. Credits: O. Grente.

The reason explaining why these studies were not based on field experimentation is because of the difficulty to implement such a protocol for large predators in the wild. An experimental study requires to control a large number of factors over large areas. In addition, the legal context to kill a protected species for scientific purposes is complicated [133].

On the other hand, it is much easier to use data about the applications of lethal control that were collected as part of a management plan. These data therefore did not follow a scientific protocol (see margin box 'Experimental studies'). Not only there was no randomisation in the distribution of the lethal removals, but the application of removals has no obligation to follow a strict protocol and the data collection could also be different among farms [133].

Experimental studies

Experimental studies requires to compare two different groups: (1) flocks are subjected to lethal protective measures, and (2) they are not. The distribution of flocks between group (1) or (2) has to be random. The application of lethal measures has to follow an identical protocol for all flocks of (1). The collection of results must be rigorously similar for both groups [133].

Analyses of these data are called **retrospective studies**. The non-respect of the experimental protocol introduces biases in the analysis [133]. When comparing flocks or areas with application of predator removals, against those without, there is a risk for what is called '*confounding factors*'. More explicitly, you could think the effect you observed in the farms with removals was due to the removals, while it could be due to another variable. For example, if the farms with removals were all located near wolf dens when the farms without removals were not, then the differences of depredation levels between the two groups could be due to the distance to den rather than to the removals.

Scientists can try to correct for this bias *a posteriori* of the data collection. This involves having access to the data potentially related to the depredation level (for example the level of non-lethal protective measures of flocks, the density of wolves, of packs etc...), which are generally not available. Even when these data are available, *a posteriori* correction is tricky [139].

[139]: Westfall et al. (2016), 'Statistically Controlling for Confounding Constructs Is Harder than You Think'

Contradictory results

The results of studies of Axis III are contradictory (reviewed in [124]). Some showed efficiency of lethal removals to reduce the depredation level, some showed no effect and finally some showed a counterproductive effect of lethal removals, where these measures increased the depredation level.

We could consider that both assumptions 1 and 2 were true but in different contexts. However, when focusing on wolves, all studies of Axis III used data from North America except one [67]. Sometimes, studies used the exact same dataset and concluded differently on the effect of lethal removals of wolves ([100, 140, 141]).

Therefore, the discrepancies in the results of these studies could emerge from the bias induced by the use of retrospective data and the risks of confounding factors [132, 133].

[100]: Wielgus et al. (2014), 'Effects of Wolf Mortality on Livestock Depredations'
[140]: Kompaniyets et al. (2017), 'Modeling the Relationship between Wolf Control and Cattle Depredation'
[141]: Poudyal et al. (2016), 'Wolf Lethal Control and Livestock Depredations'

Organisation of the PhD thesis

Context, objectives and collaborations

My PhD thesis was funded by the Office Français de la Biodiversité (OFB), the public organism in charge of the wolf monitoring and of certain aspects of the management of its depredations in France. The funds were made in the context of the National Wolf Management Plan of 2018-2023.

More precisely, the PhD project referred to Action 7.5 '***Evaluate the effect on predation of the culling decrees provided by prefects and of the culling of wolves [in France]***' [77].The increased number of culled wolves (Figure 0.12) made it possible to plan a statistical analysis of the effects of culling in France.

My PhD thesis was co-supervised by **Christophe Duchamp** of the OFB for his expertise regarding wolf biology and the wolf situation in France, and by **Dr. Olivier Gimenez** and **Dr. Simon Chamaillé-Jammes** of the Center in Functional and Evolutionary Ecology (CEFE) of the National Center for Scientific Research (CNRS), who brought expertise regarding statistical analyses applied to large carnivore ecology. Their help, advice and support as well as their complementarity has simply been absolutely essential to the achievement of this work.

We focused the thesis exclusively on the effect on predation of the culling of wolves and did not analyse the prefect decrees. As a first step, we chose two paths to study the effect of wolf culling on depredation levels:

- The study of the direct effect of culling on depredation levels in France:

As planned in Action 7.5, we used the data of culling and the data of depredations compiled by the French administration from 2011 to 2020, to study the effect of culling in France, through the application of an **analysis of Axis III** (the study of the direct effect of lethal removals of wolves on the depredation levels, Figure 3.1). The use of retrospective data made impossible to reach the scientific standard of experimental studies [133]. However, in order to deal with flaws of retrospective studies as best as we can, given the available data, we applied a methodology that has never been used in the studies of Axis III until now.

- The study of the depredation behaviour and its interactions with lethal measures :

We chose a modelling approach to study the effects of lethal measures by integrating Axis I (Figure 0.15a) and Axis II (Figure 0.15b) in the same model, in addition to the loopback effect of depredation on lethal measures. In other words, we modelled **the entire loop of the functioning of lethal removals of wolves** represented in Figure 0.14. The aim was not to provide a model for management for France (*e.g.* to determine an optimal culling quota) but to understand the mechanisms of depredation in wolves and its interactions with lethal measures. This model intended to give some clues regarding the two assumptions 1 and 2 about the effects of lethal removals.

As a second step, we included the **spatial analysis of the depredation patterns in France** and its evolution through time, from 1995 to 2018. The effects of culling were therefore not directly studied here. However, we believed that the understanding of how depredations are structured in space is essential in the current context of limited use of lethal removals. The objectives of this part were twofold:

- Investigation of the aggregation pattern of depredation in regard to the territoriality of wolves. The goal was to understand if wolf territoriality could explain the depredation spatial pattern or not, and how this pattern changed in the course of wolf recolonisation.
- Identification of the hotspots of wolf depredations at the scale of the pastoral surfaces, by correcting for the livestock spatio-temporal distribution within these pastoral surfaces. The goal was to provide maps of hotspots which would help French managers...
  - ...to locate the spatial sets of pastoral surfaces which are part of the same hotspots, therefore responding to the same local depredation dynamic, and where management of depredations could be coordinated for a better efficiency.
  - ...to target the areas not only with high levels of depredations, but also areas where the use of pastures is restricted in time, in space, with small flocks, but still with a level of depredation significantly higher than expected (see the side note *'Administrative hotspots'*). This is complementary of the actual policy of prioritising the management on the most attacked flocks [49]: small flocks with less attacks could be set aside from this list even though they would require management attention.

Administrative hotspots

The French authorities define hotspots as the municipalities within *cercle 0* (mean of at least 15 attacks over the last three years, and all the adjacent municipalities, Figure 0.7). An administrative report [142] in 2020 signalled that this method introduces bias, with municipalities of small area being penalised.

[142]: Auvergne-Rhône-Alpes et al. (2020), *Rapport d'évaluation de l'arrêté Ministériel Expérimental Du 26 Juillet 2019 Portant Expérimentation de Diverses Dispositions En Matière de Dérogation Aux Interdictions de Destruction Pouvant Être Accordées Par Les Préfets de Département Concernant Le Loup (Canis Lupus)*

In addition to my supervisors, I was helped all along the thesis by multiple people who deserved a great deal of credit for the analyses conducted in this work. First, our study on the effects of culling on depredations in France would not be what it is without the vital support from **Dr. Thomas Opitz** from the Biostatistics and Spatial processes laboratory of INRAE in Avignon. Second, the modelling approach of the whole functioning of lethal measures would simply not have been possible without **Dr. Sarah Bauduin** from the OFB and **Dr. Nina Santostasi** of Sapienza University of Rome. Finally, the study of spatial analysis of the depredation patterns in France resulted from the first work of **Thibault Saubusse**, and we were both wisely advised by **Eric Marboutin** from the OFB.

Moreover, my frequent exchanges with people from the OFB during my PhD greatly helped me to grasp the situation of the grey wolf in France in various ways. I participated to various meetings organised by *Réseau Loup-Lynx*, notably with its coordinator **Nicolas Jean** and the regional animators **Matthis Petit** and **Elsa Barrandon**. My discussions with the research team *Loup-Lynx* of the OFB, notably **Dr. Nolwenn Drouet-Hoguet**, **Dr. Ricardo Simon**, **Yannick Léonard** and **Pierre-Emmanuel Briaudet** were very fruitful in many ways. My supervisors and I also exchanged multiple times with the group of researchers Coadapht (**Dr. Michel Meuret**, **Dr. Laurent Garde**, **Dr. Nicolas Lescureux**, **Dr. Olivier Bonnet**, **Dr. Marie-Odile Nozières-Petit**, **Dr. Charles-Henri Moulin** and **Frédéric Bray**) who brought their expertise regarding the interaction

between pastoralism and wolves, and helped me to seize the situation of livestock owners in the context of predation.

One-off exchanges with people with experience regarding wolves or wolf depredations were equally fruitful. **Gérard Millischer** and **Patrick Orméa** of the Mercantour National Park, **Jean-Marc Landry** and **Jean-Luc Borelli** from IPRA and the livestock owners **Henri Cotton** and **Sylvain Rigeade** provided greatly useful insights regarding the wolf biology and the wolf depredation behaviour. Finally, the field experiences of *brigadiers* of the OFB and of the *lieutenant de louveterie* **Thierry Escallier** were extremely beneficial to me to understand the culling conditions and the responding wolf behaviour.

The structure and contents of chapters

There are four main chapters, each corresponding to one study.

The four chapters of the PhD thesis

Chapter 1 – The wolf population dynamic. This is the first brick of the integrated modelling of the effects of lethal removals of wolves. In this chapter, we modelled the structure and functioning of a wolf population, with population parameters from southern Europe if any. We focused on integrating biological processes that are at the basis of the assumptions on the effects of lethal removals on wolves, as pack dissolution.

Chapter 2 – The depredation behaviour. This is the second and last brick of the integrated modelling of the effects of lethal removals of wolves. In this chapter, we modelled the depredation behaviour of wolves and the management of depredation by culling. We analysed the effect of removals according to different scenarios for the depredation behaviour and for the culling.

Chapter 3 – Effects of culling on depredation. This is the retrospective study of the effects on depredation of the wolf culling management applied in France. No analysis on the effect of lethal removals on wolf population is done. We analysed the spatio-temporal distribution of the depredations around the culling events.

Chapter 4 – Hotspots of depredation. This is the spatial analysis of the annual aggregation of depredations and the statistical identification of pastoral surfaces as hotspots of depredation. We used information about the annual wolf observed distribution, the time spent on pastures by flocks, flock sizes, the surfaces and the locations of the pastures to establish the risk exposure of flocks to predation.

All chapter follows this general structure, unless indicated otherwise:

1. **Aim of the chapter**. This part briefly explains the objectives of the chapter.
2. **Literature review**. This part reviews the literature and knowledge relative to the study conducted in the chapter.
3. **Methods**. This part presents the methods of analysis of the study. If any, the datasets used in the study are presented first.
4. **Results**. This part presents the results of the study. Note that in Chapter 3, results are presented directly after their corresponding methods for a more fluid reading.
5. **Discussion and Conclusion**. These final parts discuss the results of the study relatively to the literature reviewed previously, and highlight the most important findings of the study.

Some practical advices

Each chapter can be read independently from each other. I purposely repeated some parts that were essential to the understanding of each chapter, even if it could be found in previous chapters. Only Chapter 1 and Chapter 2 are more connected, as Chapter 2 modelling includes the modelling done in Chapter 1. However, reading Chapter 2 without reading Chapter 1 does not prevent understanding.

Time is money

I recapitulated the main messages at the end of sections within green boxes as this one. If you are short of time[a], you can read from one box to another. Sometimes, I also added important information. Therefore these boxes are not only syntheses, and I recommend to read them even if you have read the whole section.

[a] and only if

All references cited for the first time in a chapter appear in the margin.

Maybe you have already noticed during your reading of the introduction, but the numeric version of the document is interactive. You can click on all the text in green*. It is the case for literature references. If you click on a literature reference, for example this one [143], it will bring you in the reference section, at the end of the document. You can easily come back to where you were in the main text because the page numbers where the reference appears (at the end of each reference line in the list) are themselves interactive. All the references to figures, tables, chapters or sections in the main text are also interactive and brings you to their spot in the manuscript.

Let's move on to Chapter 1.

* Well, except this one

Chapter One

The wolf population dynamic 1

Preamble

A breeding female wolf was culled during a summer in France. A few months later another breeding female was culled in the same area. One of the two females could have been foraying from an adjacent territory. However, another breeding female of the adjacent territory was culled during the same summer. A multiple reproduction within a single wolf territory was therefore suspected to explain the deaths of two breeding females at the same location during the same year.[a]

[a] *pers. com.* Elsa Barrandon, OFB

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1.1 Aim of the chapter

Understanding the effect of predator culling on depredations first implies to understand the predator itself. What makes the study of the effect of culling so special with *Canis lupus* is its singular population structure. Compared to many other predators, this species is described as social [31]. The sociality of an animal species has long been treated as binary: the individuals of a species are social or solitary. This could appear more complex, with a gradient of sociality. For pumas (*Puma concolor*), described as solitary, it has been showed that adults could have interactions apart from mating contrary to what we primarily thought [144]. Also described as solitary, the species of the red fox (*Vulpes vulpes*) involves a larger panel of social structures than what was thought [145, 146]. Alongside lions, wolves are commonly viewed as well representatives of the social predators because they live in packs [147]. We will see in this chapter that the sociality in the lifes of wolves is however complex too, involving alternately group and solitary phases, and, as we will see in Chapter 2, group and solitary hunting behaviours too.

The first and most straightforward effect of culling is the immediate reduction in the abundance of the culled species (*e.g.* for Eurasian wild boars *Sus scrofa* [148]). However, this reduction in the abundance can lead to unintended effects, such as increased movements of surviving individuals in the culling areas (*e.g.* for badgers *Meles meles* [149] or feral cats *Felis catus* [150]). For predators involving complex social structure, as wolves, the number of unintended effects might be increased because of the highest risks of destabilisation of social structures [133]. Therefore, the sociality in wolves challenges the study of the effect of culling.

The aim of the chapter was to provide the first brick of a theoretical model on the effects of culling of wolves on depredations, that will be completed in Chapter 2. In this chapter, we focused on the modelling of the structure and the functioning of a wolf population. Because this PhD was focused on the effects of wolf culling in France, we modelled this population dynamic as closely as possible to the functioning of the population encountered in France, given the available information in the literature. In addition, the goal of the literature review was to

[144]: Elbroch et al. (2017), 'Social Interactions in a Solitary Carnivore'

[145]: Robardet (2007), 'Étude de la transmission d'Echinococcus multilocularis dans une grande agglomération.'

[146]: Macdonald (1979), ''Helpers' in Fox Society'

[147]: Brandell et al. (2021), 'Group Density, Disease, and Season Shape Territory Size and Overlap of Social Carnivores'

[148]: Boadella et al. (2012), 'Effects of Culling Eurasian Wild Boar on the Prevalence of Mycobacterium Bovis and Aujeszky's Disease Virus'

[149]: Prentice et al. (2019), 'When to Kill a Cull: Factors Affecting the Success of Culling Wildlife for Disease Control'

[150]: Lazenby et al. (2015), 'Effects of Low-Level Culling of Feral Cats in Open Populations: A Case Study from the Forests of Southern Tasmania'

[133]: Treves et al. (2019), 'Predator Control Needs a Standard of Unbiased Randomized Experiments With Cross-Over Design'

identify the components in the wolf population dynamic that were the most likely to be disturbed by culling. If they were well documented, they could be model as thoroughly as possible. If essential information for modelling were missing for some of these components, we tested different configurations and assessed the impacts of these choices on the modelled wolf population dynamic.

The study of this chapter has been published in Ecological Modelling in 2020:

> Sarah Bauduin, Oksana Grente, Nina Luisa Santostasi, Paolo Ciucci, Christophe Duchamp, Olivier Gimenez, (2020). An individual-based model to explore the impacts of lesser-known social dynamics on wolf populations. *Ecological Modelling*,Volume 433, p.109209.

The article can be found in Appendix A. In this chapter, I added in greater details the literature review on which the study was based on, and I especially highlighted the links of this study to the more general study of the culling effects, and to France, these aspects being missing in the published article. In addition, I summarised the method and results of this article, and highlighting some results according to their interest regarding Chapter 2.

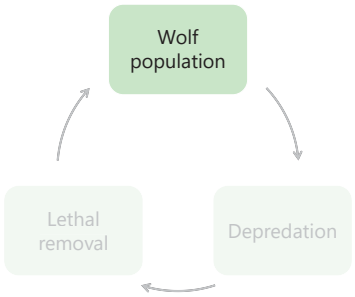

Figure 1.1: Schematic functioning of wolf depredation management by culling. The wolf population component is the component modelled in this chapter. The two other components and their interactions with the wolf population component are the subject of Chapter 2. Credits: O. Grente

To sum up

The main aim of this chapter is to model the wolf population dynamic as encountered in France, with a special attention for the components in the wolf population dynamic that were the most likely to be disturbed by culling. It is an essential first step to study the wolf culling effects on depredations.

1.2 Literature review

The wolf population dynamic without culling

The most basic social structure of a wolf population is the **breeding pair**, the association of a female and a male reproductive wolves [31] that occupies a territory that it defends against other wolves [151]. The offspring of this pair generally do not leave the pair immediately after birth and stay one or more years with the parents on the natal territory. When a breeding pair lives with its offspring, the social structure becomes the **pack**. As the number of offspring of the pair increases, totality or a part of the previous offspring leaves the pack. This process is called **dispersal** [34].

[151]: Sells et al. (2021), 'Evidence of Economical Territory Selection in a Cooperative Carnivore'

[34]: Blanco et al. (2007), 'Dispersal Patterns, Social Structure and Mortality of Wolves Living in Agricultural Habitats in Spain'

The wolf population dynamic is depending on an annual cycle (Figure 1.2). Generally, birth of pups takes place in the den during spring, as it is the case in France [12]. During summer, pups are weaned and eat meat brought by the other members of the pack. Pups stay night and day at a specific location within the wolf territory, called the *rendez-vous* site, sometimes alone when all pack's members are gone wandering in the territory or looking for food [31] [152]. Pups start to follow the rest of the

[12]: Landry (2017), *Le Loup*

[152]: Ausband et al. (2010), 'Surveying Predicted Rendezvous Sites to Monitor Gray Wolf Populations'

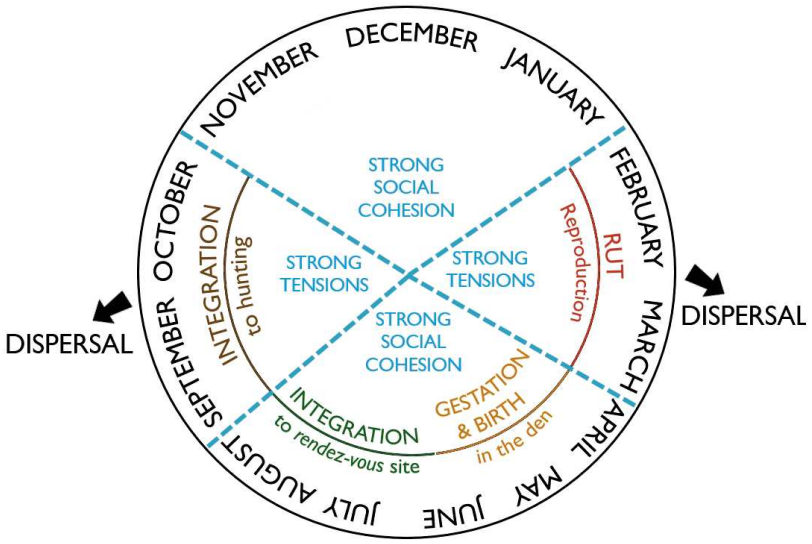

Figure 1.2: Schematic representation of the wolf annual life cycle, as observed in France. Adapted from Office Français de la Biodiversité.

pack at the end of the summer when they have grown enough, and the pack gradually abandons the *rendez-vous* site [153].

The dispersal of offspring can occur at any time of the year. However there are two main moments of the year where dispersal is the most likely to occur: during the reproduction period between winter and spring, and during autumn Figure 1.2 [154]. These are the times of the year where strong tensions between individuals can be found in the pack, relative to the competition for reproduction for the first dispersal moment, and to the competition for food for the second dispersal moment [31].

During the reproduction period, breeders are aggressive and tend to prevent the other individuals of the pack, hereafter '*subordinates*', to reproduce. This behaviour, which can trigger dispersal, explains how **multiple breeding** in packs are generally avoided [155]. However, when pack size is large and wolf population density is high, multiple breeding are recorded and common [156] [155]. It is probably more difficult in a large pack for the dominant breeders to suppress the mating behaviour of the subordinates, whether the mating is between subordinates or with one of the breeder. On the other hand, multiple breeding could be an advantage in dense populations of wolves. It has been showed that multiple breeding resulted in larger recruitment[1] of pups within packs [158], which can be useful to defend the territory against close neighbouring packs [159, 160]. At a low density of wolves, the advantages of multiple breeding become less obvious, as pup survival is higher in a small pack at low density [158]. All these results comes from the highly monitored wolf population of the Northern Rocky Mountains (NRM) in the USA (Idaho and Yellowstone National Park, YNP). Currently in the Alps, a single breeding pair per pack would be the rule [161, 162], but with the increasing density of wolves in this massif, including on the French side [29], multiple breeding could become more frequent.

Age of wolves in dispersal (hereafter '*dispersers*') varied but in multiple areas, wolves leaves the pack quite early, between the ends of their first and second year when they are subadults (also called '*yearlings*') [34] [163, 164]. In these studies, the dispersal occurred in every direction from the natal pack. No unbalanced sex-ratio was found amongst dispersers,

[153]: IPRA (2020), *Carnets d'observation : la meute sur son site de rendez-vous*

[154]: Gese et al. (1991), 'Dispersal of Wolves (Canis Lupus) in Northeastern Minnesota, 1969–1989'

[155]: Ausband (2019), 'Pair Bonds, Reproductive Success, and Rise of Alternate Mating Strategies in a Social Carnivore'

[156]: Ausband (2018), 'Multiple Breeding Individuals within Groups in a Social Carnivore'

1: *'The addition of new individuals to populations [through] the production of [offspring], their survival, and their settlement.'* [157]

[158]: Ausband et al. (2021), 'The Effect of Group Size on Reproduction in Cooperatively Breeding Gray Wolves Depends on Density'

[159]: Cubaynes et al. (2014), 'Density-Dependent Intraspecific Aggression Regulates Survival in Northern Yellowstone Wolves (Canis Lupus)'

[160]: Cassidy et al. (2015), 'Group Composition Effects on Aggressive Interpack Interactions of Gray Wolves in Yellowstone National Park'

[161]: Marucco et al. (2010), 'Predicting Spatio-Temporal Recolonization of Large Carnivore Populations and Livestock Depredation Risk'

[162]: Caniglia et al. (2014), 'Noninvasive Sampling and Genetic Variability, Pack Structure, and Dynamics in an Expanding Wolf Population'

[29]: Réseau Loup-Lynx (2021), *Bilan de suivi hivernal de la population de loups - Hiver 2020/2021*

[163]: Fuller et al. (2003), 'Wolf Population Dynamics'

[164]: Kojola et al. (2006), 'Dispersal in an Expanding Wolf Population in Finland'

nor amongst the distances of dispersal. [165] reported for the period 1993-2008 in the NRM however that males tended to disperse more but not farther than females. In other studies with an unbalanced sex-ratio amongst dispersers, it was generally males which disperse more or farther [31].

[165]: Jimenez et al. (2017), 'Wolf Dispersal in the Rocky Mountains, Western United States: 1993–2008'

Several options are possible for dispersers [31]:

- Dispersers can rejoin an existing wolf territory where a breeding place is vacant [166], whether the territory is occupied by a lone wolf of opposite sex, or a pack. These dispersers then become the breeder of the territory.
- Dispersers can rejoin a wolf territory where both breeding places are occupied. This process is called **adoption**, and the dispersers do not become the breeders of the territory but '*adoptees*'. This apparently concerns more young males in the few studies reported on the subject (see [31]), or adult males [167].
- Dispersers can settle alone in a new territory.
- Dispersers can settle at a proximity of a wolf territory by pairing with a subordinate of this territory. This process is called **budding**.

[166]: Stahler et al. (2002), 'The Acceptance of a New Breeding Male into a Wild Wolf Pack'

[167]: Jędrzejewski et al. (2005), 'Genetic Diversity and Relatedness within Packs in an Intensely Hunted Population of Wolves Canis Lupus'

Except for adoption, all these strategies enable dispersers to become breeders. When alone in a new territory, the newly established individual has to wait for a partner of the opposite sex to arrive, and should be considered as an awaiting breeder.

Dispersal should not be seen as a process happening only once in the life of a wolf. First, pre-dispersal movements outside the pack's territory, which always involve a come back to the natal pack, have been recorded, for example in Italy [168]. In Spain, pre-dispersal movements have been recorded over several dozens kilometres and lasted a couple of days [34]. In Alaska, these movements could occur over more than 50 km and could last weeks [169]. Second, dispersal can happen several times for the same individual because it can change its territory or it can leave packs [34]. It is therefore not uncommon during the early life of a wolf that it travels or wanders alone, even if the ultimate goal for any wolf is to form a breeding pair in a stable and resourceful territory.

[168]: Mancinelli et al. (2018), 'Beyond Home: Preliminary Data on Wolf Extraterritorial Forays and Dispersal in Central Italy'

[169]: van Ballenberghe (1983), 'Extraterritorial Movements and Dispersal of Wolves in Southcentral Alaska'

To become a breeder, dispersal is not the only option. Subordinates can look for opportunities within their natal territory.There has been observations of polygamy with multiple breeding females inside a pack, or with multiple breeding males [155], or even multiple breeding pairs. In the last case, this can lead to the splitting of the pack in half, especially when pack is large [31].

When a breeder dies in a pack, a subordinate can also take its place. Instead of being passive, this replacement can also be active, the subordinate challenging the position of the established breeder. If a breeder loses its place, it can stay in the pack [170, 171], or disperse to look for other breeding possibilities [172] [171], or be killed during the confrontation [173].

[170]: Mech (1995), 'A Ten-Year History of the Demography and Productivity of an Arctic Wolf Pack'

[171]: Rutledge et al. (2010), 'Protection from Harvesting Restores the Natural Social Structure of Eastern Wolf Packs'

[172]: Smith et al. (1997), 'Is Incest Common in Gray Wolf Packs?'

[173]: Messier (1985), 'Solitary Living and Extraterritorial Movements of Wolves in Relation to Social Status and Prey Abundance'

The replacement of a breeder inside the natal pack always raises the issue of incestuous mating, as generally subordinates are offspring of the breeding pair. It has been showed that wolves avoid incestuous pairing when possible [162, 167, 171, 173]. Therefore, if a breeder dies, it is admitted by biologists that a subordinate will not pair with its one surviving parent

[31], except if the subordinate was an adoptee unrelated to the surviving breeder. In this case, another subordinate, unrelated to the surviving breeder can fill the vacant place and pair with it. Similarly, the process can be done with a disperser, which can pair with the surviving breeder or a subordinate [162].

Thus, there are many possible configurations for breeder replacement when a breeder dies [162]. However, in certain cases, the breeder is not replaced and the **pack dissolves**, meaning that its surviving members promptly died or left after the breeder's death [174]. This vacant place can benefit to neighbouring packs which can extend their territories, or to dispersers by giving close settlement opportunity. Indeed, because of aggressiveness of wolves towards outsiders [175], dispersal is a risky process for wolves, especially in saturated areas where they are likely to encounter established packs. It has been showed in the NRM [165] that the disperser rate is decreasing with pack density. This result and the studies on multiple breeding reproduction mentioned earlier suggested that in saturated areas, it could become more profitable for subordinates to wait for a breeding opportunity within their pack rather than leave. On the contrary, dispersal could be more profitable in recolonising population where settlement on a close and vacant territory is easy [162]. This is probably the process which explains why pack size increases with wolf and pack densities at first[2]. Then, large pack sizes in saturated areas could uphold because of a better defence of the pack territory and therefore of resources against other packs [159, 160].

[174]: Brainerd et al. (2008), 'The Effects of Breeder Loss on Wolves'

[175]: Smith et al. (2015), 'Infanticide in Wolves: Seasonality of Mortalities and Attacks at Dens Support Evolution of Territoriality'

2: Quoted from [31]: '*Based on two studies [...], the spatial changes that take place as wolf populations colonize or recolonize an area are as follows. First, pairs form large territories and breed. Then pack size increases, territory size declines, and the number of territories increases.*'

The strategy to choose between leaving and waiting in the pack could also be different among sexes, according to the signal sent by several studies from various locations. Thus, females would tend to replace the breeding females within their natal pack, whether it is in Italy [162] or in Poland [167], when males were frequently observed replacing a breeder in another pack, as in the USA [176]. This is not consistent with the general findings of unbiased sex-ratio amongst dispersers, at least if we consider that both sexes have similar mortality rates, and therefore the same opportunities for replacement. However, maybe studies have for now never succeeded to statistically confirm that dispersal is sex-biased. Currently in France, most monitored wolves that have dispersed far from the Alps, to the Massif Central or the Pyrenees, were or are males (M. Petit, OFB, *pers. com.*), therefore supporting the sex-biased breeding strategy in France.

[176]: Vonholdt et al. (2008), 'The Genealogy and Genetic Viability of Reintroduced Yellowstone Grey Wolves'

The key message on wolf population dynamic

To conclude, a large variety of breeding opportunities is possible for wolves [176]. Reproduction and food competition leads to intraspecific strife between individuals of the same pack, fuelling dispersal. Meanwhile, this competition also leads to intraspecific strife between packs, which decreases dispersal profitability and leads to larger packs in saturated areas. Breeding pair turnover and pack turnover are thus naturally part of the wolf population dynamic.

For the study of the culling effects, the first issue will be to disentangle this natural population dynamic and the disruptions added by culling. The second issue will be to assess how much the culling disruptions

interfere with the population functioning and the wolf depredation behaviour. Moreover, most of the studies on the wolf population dynamic were based on populations in North America. It will therefore be a supplementary challenge to study the culling effect on the French wolf population.

Wolf population dynamic disruptions

Culling is an artificial form of mortality. Part of the culled wolves could have naturally died the same year as the year of their culling if they would not have been culled. In this case, we talk about **compensatory mortality**. The effects of culling on the population dynamic would then be limited. In short, the disruptions caused by the deaths of the culled wolves would have appear anyway. Compensatory mortality suggests that culling targets the individuals with the highest risks of mortality: the weakest (very young or very old) or the wolves the most exposed to mortality, for example the dispersers because they are exposed to intraspecific strife [34, 161].

However, culling can target the most depredating individuals if it is applied during an attempt of depredation, or culling can target any wolf if it is classic hunting. Thus, the categories of wolves with the highest survival rates, which are the adults in a pack (regardless of the breeding status), can be as much affected by culling as the others. Therefore, we do not expect culling to be a form of compensatory mortality, but rather of **additive mortality**, as it has been showed for wolf populations in North America [177] [171]. Contrary to compensatory mortality, the disruptions caused an additive mortality due to culling would not have appeared without culling.

[177]: Creel et al. (2010), 'Meta-Analysis of Relationships between Human Offtake, Total Mortality and Population Dynamics of Gray Wolves (Canis Lupus)'

Moreover, the amplitude of the disruptions also depends on the status of the culled wolves. Breeding wolves have a larger role in the stability of the wolf population structure than the other wolves [42]. Thus, because culling may kill breeders additively to natural mortality, culling may result in higher population instability.As we have seen, the death of a breeder can result in two main options for the pack: mostly, the pair is replaced, partially or totally, and in some cases, the pack dissolves [174]. Therefore, the most striking risk of disruption caused by culling is a higher rate of pack dissolution. In a meta-analysis, [174] showed that the deaths of one or two breeders in a pack, mostly caused by culling in the study dataset, could result in a dissolution of the pack in 37% of the studied cases. The sex of the lost breeder did not influence the dissolution process, but the number of lost breeders per pack did. Thus, the risk for pack dissolution was of 26% only with one lost breeder, and of 85% with two lost breeders.

[42]: Milleret et al. (2017), 'Let's Stay Together?'

However, other parameters could influence pack dissolution. The study of [174] showed that smaller packs (2–3 wolves) after the breeder loss significantly having higher risks of dissolution compared to large packs (5–6 wolves). The study also showed that smaller packs were less likely to provide sufficient care for the remaining pups in the case of a breeder loss, but also to fill the breeder place with a wolf internal to the pack. This explained why pack dissolution was higher for small than large packs.

Finally, the pack dissolution process was also dependent on the level of saturation of the area [174]. A breeder loss is likely to be quickly replaced in the presence of neighbouring reproductive packs, therefore minimising the risks for dissolution or delayed reproduction. We therefore do not expect culling to have the same disruptive effects according to the population density, the risks being minimised for saturated populations compared to small and recolonising populations.

Therefore, breeder loss did not result in pack dissolution in 63% of the studied cases [174]. This did not mean that there was no changes in these packs (except the replacement of the lost breeder) on the short term. First, the same study showed that the remaining packs could split or bud. Yet these cases were anecdotal (6.5% of 123 analysed breeder losses). Second, [178] showed in Idaho that the loss of the breeding female in a pack was significantly associated with an increase in the number of pups of the pack the next year. This could appear surprising, especially when [174] showed that reproduction could be negatively affected by the breeder loss in small packs. However, the analysed packs in [178] would be considered large in [174]. The phenomenon underlying the surprising result of [178] was in fact the raise in the number of breeding females in the pack, in other words the raise in multiple breeding. This is consistent with findings from [156] that multiple breeding was more common in large packs. Interestingly, the loss of a breeding male had not the same effect on multiple breeding in [178].

[178]: Ausband et al. (2017), 'Effects of Breeder Turnover and Harvest on Group Composition and Recruitment in a Social Carnivore'

The consequences of breeder replacement can also occur on the long term. Culling is likely to shorten breeding pair duration [42, 167], and to decrease the age of first reproduction [179]. This can be problematic as [155] showed that the duration of a breeding pair and the age of the oldest breeder significantly increased pup survival. Moreover, multiple breeding, especially multiple breeding females, was less likely to occur in packs of which the breeding pairs last longer [155]. By reducing the size of packs [178], culling may however limit risks for multiple breeding. However, the reduction of size induced by culling could in turn increase the risks for pack dissolution, whether the breeder losses were due to culling or due to natural causes [174]. This assumption could explain why adoption was more frequent in areas with culling, in Canada [171] or in Belarus [167]: pack dissolution fuels dispersal and small packs could be more likely to adopt dispersers.

[179]: Wikenros et al. (2021), 'Age at First Reproduction in Wolves'

The culling effects at the pack and population levels.

To conclude, because of the increased mortality rate of breeders under culling, the wolf population dynamic is likely to be accelerated under culling, with more turn over of breeding pair or of entire pack. More studies are however required to formally assess with certainty the role of culling in these processes at the pack level. For example, [178] and [155] did not show a significant effect of culling on the frequency of breeder replacement or of culling rate on breeding pair duration. [42] and in a certain extent [167] gave insights of the role of culling in breeding pair replacement but without making comparison with periods without culling.

The effects of culling may be varied and may depend on the context

at the population level. In wolf populations of low density, where packs are likely smaller, pack dissolution risks will probably be higher because of culling. In saturated population, where pack size is likely higher, replacement of lost breeders will probably be quicker, but the disturbance of breeding pair stability may favour multiple breeding, and therefore increase natality rates. For example, in the NRM [177] and in Alaska, [85], natality increased when the population was controlled by culling, but natality was not enough to compensate for the additional mortality caused by culling. The ratio between natality and mortality of wolf populations was also more fluctuating during periods of culling in Alaska [85] and in Canada [171].

[85]: Schmidt et al. (2017), 'Effects of Control on the Dynamics of an Adjacent Protected Wolf Population in Interior Alaska'

Therefore, if the effects of culling on the population dynamic have been assessed, they are less known at the pack level.

1.3 Modelling

As said earlier, the aim of the chapter was to model the structure and the functioning of a wolf population, in order to later integrate the depredation and culling components to the model. Thus, the model would allow us to observe the effects of culling on the wolf population and the repercussions on the depredation levels.

The Individual-Based Model (IBM)

When you attempt to model an animal population as a population of grey wolves, you mainly have two options.

The first option is to model the population as a whole, through what modellers call a **population model**. In this type of model, there is no modelling of each individual of the population. What is modelled are the demographic rates of the population: the population size, the growth rate of the population or the survival rate of its individuals. Some population models can go into deeper details and cut the population into different categories. For example, the wolf population modelled in [180] classifies the wolves into four categories: juveniles, dispersers, subordinates and breeders. However, the population models aim to stay simple by reducing the modelled processes as most as possible. For example in [180], there is no modelling of sex, and therefore of breeding pairs. In population models, the transitions of sets of individuals from one category to another are modelled, but there is no life record of each individual over time [181]. To conclude, the interest of these models lies in the parameters at the population-level, modelled through minimal individual processes.

[180]: Marescot et al. (2012), 'Reducing Matrix Population Models with Application to Social Animal Species'

[181]: Chandler et al. (2021), 'Spatial Capture-Recapture and a General Framework for Individual-Based Models of Population Dynamics'

The second option is to model each individual of the population, through what modellers call an **Individual-Based Model (IBM)** (also called '*agent-based model*'). In IBMs, each individual and its characteristics, for example its age or its sex, are explicitly modelled. Consequently, biological processes happening at the individual-level, such as the formation of the breeding pair, or the replacement of a lost breeder, can be modelled in an IBM, whereas it is often impossible in a population model. The interest of IBMs lies in the modelling of the mechanisms happening at the individual level in order to see the consequences at the population level. This type

of modelling is called mechanistic [182]. It is opposed to empirical modelling which describes what is observed at the level of interest (*e.g.* population-level) by mostly staying at the level of interest (Equation 1), as in the population model of [180]. The description in empirical modelling is generally mathematical, through the use of equations, whereas in mechanistic models, the explicit use of mathematics can be done for all or part of the modelled mechanisms but is not compulsory [182].

[182]: Thakur (1991), 'Model: Mechanistic vs Empirical'

Definition 1 *A **mechanistic model** describes, quantitatively or not, what happens at one level (e.g. population-level) by considering the mechanisms occurring at lower levels (e.g. individual-level). An **empirical model** describes what happens at one level quantitatively (i.e. with mathematical equations) with information from the same level. [182] [183].*

[183]: Marion et al. (2008), *An Introduction to Mathematical Modelling*

Mechanistic models generally require a certain amount of knowledge about the mechanisms occurring at the lower level. Usually, they are not known in great details. This partly explains why empirical models are more popular than mechanistic models for population ecology modelling [181]. In addition, according to the studied system, mechanistic models can be complicated to handle compared to empirical models, and scientists can simply not be interested by the underlying mechanisms of what they study [182].

In our study, we are however lucky. The grey wolf is a well-known species, with a great amount of literature regarding its biology. The book of [31] which reviewed the studies on grey wolves across the world runs over 448 pages. The book has been published 18 years ago. Since, many studies about grey wolves are published every year (Figure 1.3).

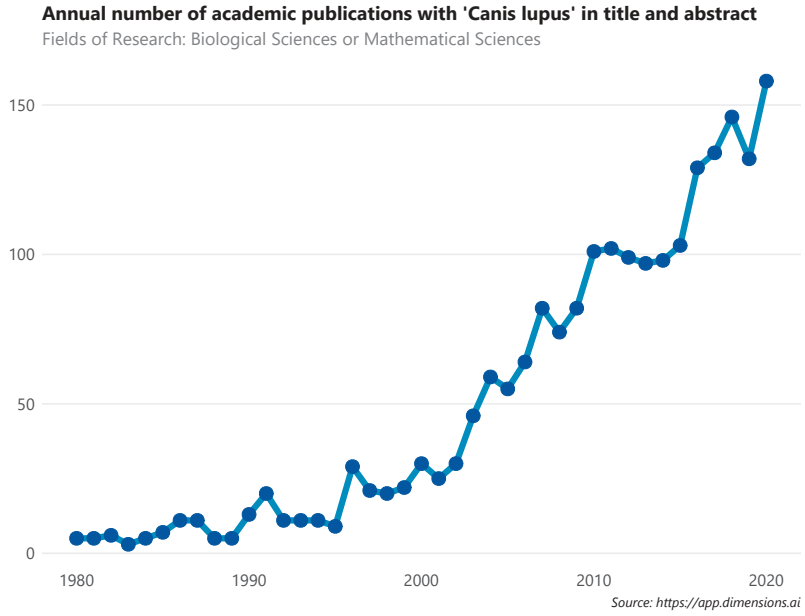

Figure 1.3: Annual number of academic publications with '*Canis lupus*' in title and abstract for fields of Biological Sciences or Mathematical Sciences from 1980 to 2020. Source: https://app.dimensions.ai. Credits: O. Grente

It is true that there are wolf populations that are over-represented in these studies [184], as North-American populations, such as the highly monitored wolves from the YNP [160]. Population parameters derived from North America may not represent the dynamics found in Europe or in France. However, we can expect that the biological mechanisms

[184]: Marescot (2012), 'Dynamique et Conservation Des Populations Difficilement Observables : Cas d'étude de La Recolonisation Du Loup Dans Les Alpes Françaises'

underlying population dynamics are equivalent to what is found for the European species. Therefore, we could favour the information provided by studies on the European populations of grey wolves, especially those close to France (*i.e.* in the Italian Alpine region), but the potentially necessary extension to the studies about North American populations when modelling the biological mechanisms could still make sense.

Why IBM?

The complex social structure of grey wolves, as we have seen in the literature review of this chapter, needs to be taking into consideration to test the Assumptions 1 and 2 presented at the end of the Introduction. The final aim of the model, once completed, was to understand the mechanisms of depredation of wolves and the interactions of wolves with lethal measures. The depredation behaviour, as we will see in Chapter 2, required to model the depredation behaviour of each wolf based on multiple individual characteristics.

Consequently, we decided to use an Individual-Based-Model (IBM) to model the wolf population and thereafter its interactions with depredations and lethal removals. This modelling technique is mechanistic: it allows the explicit consideration of the biological mechanisms (as pack dissolution) to understand the overall functioning (as the lethal removal effects), by modelling each individual of the population. Such approach would have been impossible with empirical population models.

Before us, other studies on grey wolves already opted for IBMs instead of population models. In regard to what we have seen in Introduction, they could be related to Axis I (The study of the effect of lethal removal on wolf population) [111, 185, 186], or Axis II (The study of the relationship between wolf population structure and depredation level) [161] or finally to monitoring purposes [187].

[111]: Chapron et al. (2003), 'Conservation and Control Strategies for the Wolf (Canis Lupus) in Western Europe Based on Demographic Models'
[185]: Bull et al. (2009), 'Survival on the Border: A Population Model to Evaluate Management Options for Norway's Wolves Canis Lupus'
[186]: Haight et al. (2002), 'Computer Simulation of Wolf-Removal Strategies for Animal Damage Control'

[187]: Chapron et al. (2016), 'Estimating Wolf (Canis Lupus) Population Size from Number of Packs and an Individual Based Model'

To be spatial or not to be spatial?

Once we chose the individual-based modelling, the adventure only began and a large choices of modelling were still in front of us. The first choice was linked to the modelled area. We could decide to model France or its Alpine region. In this case, the IBM would have been spatially explicit. It would have allowed the explicitly modelling of the dispersal movements of wolves, or of the encounters between wolves and livestock.

However, we thought that using a spatially explicit IBM could not be beneficial for several reasons. First, modelling an area requires spatial data, such as forest cover, pastoral surfaces, towns, roads etc... These data are available but would have require a non-negligible amount of time to assemble them and to make sure they are consistent, as they generally originate from different sources, themselves of different times.

Second, the focus of our model was not to predict dispersal or recolonisation, as in [161], that require the explicit use of spatial data. Moreover, **our study did not aim to predict depredation or lethal removal effect at specific areas of France too**. Indeed, the goal of our study was neither

to predict nor to understand the effects of lethal removals according to very specific environmental parameters, for example the proportion of forest cover or the slope of pastures. The reason for this is the infinity of environmental parameter combinations, not only for the data that we have at our disposal, but also for all the data that we do not have, or that we have not thought to. The goal was the understanding of the big picture of the whole dynamic *culling-wolf-depredation* (Figure 0.14), in a **fictional environmental and pastoral context**. More details about this important point will come in Chapter 2.

Third, there was a simple method to consider spatiality in the IBM without explicitly modelling an area. For that, we used the territoriality of wolves. In the IBM, each individual, if it was resident, belonged to one territory (alone or with other wolves of its pack). Because resident wolves are highly territorial, the modelling of rules relative to packs mimics the area. These are some examples of these rules that we included:

- There is a maximum number of possible territories that can be formed in the model (hereafter '*carrying capacity*').
- The more packs there are in the model, the less chance for dispersers to create a new territory (alone or with another disperser), in order to mimic the difficulty to settle for wolves in a saturated area.
- The mortality becomes density-dependent once all the territories have been occupied. This mimicked the results of [159] in the YNP, where wolf density '*regulated adult survival through an increase in intraspecific aggression, independent of prey availability*'.

[159]: Cubaynes et al. (2014), 'Density-Dependent Intraspecific Aggression Regulates Survival in Northern Yellowstone Wolves (Canis Lupus)'

Finally, a spatially implicit IBM had also a final advantage: its adaptability. The model of the wolf population we made could be re-used by other scientists in other contexts, for other areas. Indeed, by changing a few parameters, especially the maximum number of possible territories of the model, the model I present in this chapter can be easily adaptable to model any grey wolf population, or could be updated with new or more adapted parameters.

Special yes but spatial no

We decided to model a **non-spatial IBM**. The reason for this is first to simplify the model in order to allow room for the complexities which will follow, in short the biological processes inherent to wolf sociality, and thereafter the wolf depredation behaviour. Second, the spatiality was implicitly modelled, through the affiliations of individuals to packs and the use of rules related to the maximum pack number.

The basic modelled processes of wolf life cycle

There are some basic biological processes that are well known for grey wolves, that were mentioned previously in the literature review of this chapter. They are included in most if not all IBMs of grey wolves. All of these processes are included in our model.

- The reproduction of breeding pairs
- The aging of wolves
- The mortality of wolves

- The dispersal of wolves
- The immigration or emigration
- The creation of new pack by a breeding pair on a new territory
- The establishment of a lone wolf on a new territory

We did not have at our disposal the parameters for the wolf population in France for these processes (*e.g.* the number of pups produced per litter, the mortality of wolves per age class or per resident status...).

This is why we had to incorporate some parameters estimated from the intensive monitoring sessions of other wolf populations for the modelling of the reproduction, the mortality and the dispersal processes (Table 1.1).

Table 1.1: Parameters used in the IBM for the Reproduction (Repro.), Mortality (Mort.) and Dispersal (Disp.) processes of the wolf life cycle. DD stands for density-dependence. NRM stands for Northern Rocky Mountain area and YNP for Yellowstone National Park, which are both in the USA. W. Italian Alps stands for Western Italian Alps. Population column refers to the wolf population from the Reference column. Adapted from Table 1, p.18 of [191], also available in Appendix A.

Parameter	Process	Explanation	Value	Reference	Population
Litter size	Repro.	Mean of a Poisson distribution generating the number of pups produced by a breeding pair.	6.1	[188]	Belarus
Relatedness	Repro.	The formation of a breeding pair favours two individuals with a relatedness coefficient lower than this threshold.	0.125	[162]	Northern Apennines
Pup mort.	Mort.	Mortality probability for wolves in their first year of life.	0.602	[189]	NRM
Res. mort.	Mort.	Mortality probability for resident wolves after their first year of their life.	0.18 ($sd = 0.04$)	[190]	W. Italian Alps
Disp. mort.	Mort.	Mortality probability for dispersers (except dispersing pups).	0.31	[34]	Northwest Spain
DD resident adult mort.	Mort.	Mortality probability for resident adults when the population is at carrying capacity as: $logit(\phi) = a + b \times ((\frac{N_w}{C_c \times T_s} - c)/d)$ where N_w is the number of wolves without pups, C_c the carrying capacity and T_s the territory size.	$a = -1.2$ $b = -0.5$ $c = 53.83$ $d = 17.98$	[159]	YNP
Terr. size T_s	Mort.	Used for the density-dependent resident adult mortality.	104 km^2	[168]	Abruzzo
Pack size	Disp.	Mean of a Normal distribution generating the annual maximum size of each pack.	4.405 ($sd = 1.251$)	[161]	W. Italian Alps

Regarding dispersal, we completed these parameters with information from [86] and [31], where it is mentioned that the oldest non-breeding individuals of the pack have the highest risks to leave the pack because of competition for food and reproduction. Dispersal was triggered when the pack size was above the maximum number of wolves it could sustain (see Pack size in Table 1.1).

[86]: Haight et al. (1997), 'Computer Simulation of Vasectomy for Wolf Control'

The lesser-known modelled processes of wolf life cycle

In previous IBMs on grey wolf, there was some processes of the wolf life cycle that were not included. The reason for this is that they are less documented than the processes previously mentioned. These processes relate directly with Assumptions 1 and 2 about the lethal removal effect.

- *The pack dissolution*: This process is the general concern of Assumption 2, where it is assumed that pack dissolution is increased by culling, therefore increasing risks of disruptions of the population social structure. The risk is increased for small packs [174].
- *The adoption of young lone wolves into pack [31]*: Adoption is more frequent in area with culling [167, 171]. Adoption of a young wolf can accelerate the replacement of a lost breeder in the future, and increase the survival of young dispersing wolves.
- *The formation of a pack through budding [31]*: This process can accelerate the formation of new territories and can increase the survival of wolves by decreasing the frequency of dispersers in the population (dispersers have a lower survival rate [34]).
- *The sex-biased replacement of lost breeder by subordinates*: There could be a different breeding strategy between females and males. It has been observed that females could favour the breeding strategy to wait in the pack in order to replace the breeding female [162, 167], whereas males could tend to favour dispersal and establishment outside their natal pack [176]. This can have consequences on the dynamic of reproduction, with more males among dispersers.
- *Multiple breeding*: The loss of a breeder can cause multiple breeding within a pack, especially within large packs and within dense wolf populations [155, 156].
- *The pack density*: The increase in pack density can result in a lower rate of dispersers [165] and can result in an increase in pack size [31], favouring multiple breeding [156].
- *The pack splitting*: Multiple breeding could lead to pack splitting [31]. In addition, a territory of at least 3 wolves could also split in half after the loss of a breeder instead of dissolving [174].

The implementation of these processes in our model would allow the wolf population model to be more realistic, especially when we will consider the effect of lethal removals thereafter. However, as said, these processes are poorly documented. For most of them, we had no idea of the frequency of their occurrence in the wild.

Consequently, to implement these processes in our model, this required to test different parameters or different combinations for these processes in our model. Each time a parameter was tested, it created a different version of the model. We called a version of the model a *scenario*.

Definition 2 *A **scenario** is a version of a model that is unique, because the version involves a different set of parameters than the others versions, or a different layout of the modelled processes.*

A lot of processes in our model were stochastic. This meant that the value they produced (*e.g.* the number of pups produced by a breeding pair) was not known in advance because the value was drawn in a

distribution (*i.e.* a set of possible values, the values not having necessarily the same probability of being drawn). There was a risk that only extreme values were drawn, therefore not reflecting the general tendency that we expected from our model. A more thorough explanation of stochasticity is provided in Appendix B of the thesis.

The stochastic side of our model meant that we could not rely on one replication: we had to run a lot of replications to avoid risks of unrepresentative results. Because each scenario corresponded to a model, this meant that a lot of replications had to be done for each scenario.

These needs for replications for each scenario greatly limited the study. Let's take an example. I want to test three probability values for a pack to adopt a lone wolf: A_1, A_2 and A_3. But I also want to test three different probabilities of budding for a disperser: B_1, B_2 and B_3. Therefore, there are 3parameters $\times$ 3parameters $=$ 9 combinations possible of A and B values, so 9 possible scenarios. If I add four new parameters for another process, the number of scenarios increases from 9 to $3 \times 3 \times 4 = 36$. Now, I have to replicate each scenario a large number of times, let's say 200 times. So I would have to run $36 \times 200 = 7200$ simulations.

The dark side of IBMs compared to other types of modelling is the time that they can take to run. The more complex they are, the longer it will take. Therefore, increasing the number of processes to test does not only increase the number of simulations, but it can also increase the duration of each simulation. In addition, the multiplication of the number of scenarios makes the analysis of the results more and more complicated.

For these reasons, we therefore decided to limit the number of lesser-known process to implement in the model, but also the number of parameters to test for the chosen processes.

Among the lesser-known processes of the wolf life cycle that we identified, and that can impact the effects of lethal removal on the wolf population structure and dynamics, we tested in our IBM the four following processes:

- **Pack dissolution**. We based our modelling on the meta-analysis of [174].
  - The results of [174] showed that the risks for packs to dissolve was higher for small packs compared to large packs. They did not define a threshold between small and large packs but calculated that the packs which dissolved contained on average 2.36 individuals after breeder loss ($sd = 3.18$), whereas packs which did not dissolve contained on average 5.75 individuals after breeder loss ($sd = 4.74$). For simplicity, we modelled that only small packs could dissolve. **To define if a pack was small or not, we tested three parameters: 4.1 *(mean between 2.36 and 5.75 from [174])*, 3.1 and 5.1.**
  - The results of [174] showed that risks of pack dissolution were higher when the two breeders were lost (84.6%) than when only one breeder was last (25.8%). We therefore used a probability for small packs to dissolve of 0.846 if the two breeders died, and of 0.258 if only one breeder died.

- **Adoption**. Consistently with findings reviewed in [31], we modelled that packs could only adopt young individuals between 1 and 3 years old (inclusive), and in priority males. In our model, packs had a limited size that could vary across time (to reflect fluctuating resources on the pack's territory). Therefore, packs could only adopt individuals according to their current limited size, if there was room for adopting an individual. The rate at which adoption occurs in the wild was however unknown. To explore how relevant this process is to affect wolf population dynamics, **we tested three probability values for a pack to adopt a disperser between 1–3 years old if the pack size was below its maximum size: 0.1, 0.5 and 0.9**.
- **Budding**. Along with the creation of new territory alone or with another breeder (in the section *The basic modelled processes of wolf life cycle*), budding was the third possibility for a wolf of our model to create a new territory. The creation of a new territory in our model, whether it was by pair, alone or by budding, was always density-dependent (the more packs, the less likely to form a new territory) and was always between two unrelated individuals (for a relatedness value of 0.125, Table 1.1). The frequency of budding, compared to creation of a new territory by a pair or a lone wolf, was unknown in the wild. **We tested three probability values for a disperser to successfully bud with a subordinate: 0.1, 0.5 and 0.9**.
- **The sex-biased replacement of lost breeders**. In our model, the replacement of a breeder could be done by a disperser or a subordinate. In the first case, the disperser must be unrelated to the surviving breeder (if any). In the second case, the subordinate the least related to the surviving breeder (if any) replaced the lost partner. As said earlier, there was no certainty about the most frequent type of replacement of breeder and if it was different between sexes in the wild. **We tested three different layouts:**
  - **Version M1:** Female subordinates were favoured over female dispersers to replace lost female breeders. Male dispersers were favoured over male subordinates to replace lost male breeders.
  - **Version M2:** Subordinates were favoured over dispersers to replace lost breeders for both sexes.
  - **Version M3:** Dispersers were favoured over subordinates to replace lost breeders for both sexes.

For each of these four tested processes, we had $3^4 = 81$ scenarios to test. To limit the number of scenarios,we decided to let aside the three remaining processes about **multiple breeding**, **pack density** and **pack splitting** mentioned earlier.

The reason for this choice was the focus we made on the Alpine wolf populations. Multiple breeding and pack splitting were generally reported for dense population where large packs were frequent, as in some areas of North America ([31], [158], packs of $\geqslant 8$ adults in YNP for a 5.5 wolves per 100 km^2). In Europe, the density of wolves is generally lower, with an estimation at 0.9–1.1 wolves per 100 km^2 in the Italian Alps in 2014–2015 [192]. In this area, the unique breeding pairs within pack apparently apparently stays the rule [161, 162].

[192]: Marucco et al. (2016), 'The Wolf Population Status in the Italian Alps'

This choice is debatable given the increasing density of wolves and packs in the French side. Consequently occurrences for multiple breeding and pack splitting should be increasing too. This will be more thoroughly discussed in section *A French scenario?* in Chapter 2.

The 13 modelled processes of wolf life cycle

We modelled 7 processes that had already been integrated in most IBMs related to grey wolves: *reproduction*, *aging*, *mortality*, *dispersal*, *immigration/emigration*, *creation of a new pack by a breeding pair on a new territory* and *establishment of a lone wolf on a new territory*.

We also added 4 lesser-known processes that had never been integrated into IBMs of grey wolves: *pack dissolution*, *adoption*, *budding* and *sex-biased replacement of lost breeders*. These processes had been documented several times in different studies, but there are still uncertainty surrounding their behaviour and their frequency of occurrence. However, incorporating them was an important step to study the effect of lethal removal on the wolf population structure, as these processes could modify the level of disruptions caused by lethal removals.

Because of the high number of simulations required by the implementation of the lesser-known processes, we voluntarily let aside the three remaining processes about **multiple breeding**, **pack density** and **pack splitting** of the wolf population dynamic, as they were supposedly less encountered in the Alpine region.

The model structure

Thus, our IBM of wolf population was composed by 13 processes. All the individuals of the population successively moved from one process to another. Each process could be seen as a submodel, with its own set of rules. I gave you a glimpse of their rules in the last two sections, but I refer you to our published article [191] for all the details of modelling (the article is also available in Appendix A of the thesis).

Once the individuals completed the 13 processes, they started a new cycle, where they had again to go through all the processes. **A cycle mimics one year** from spring where reproduction occured, to the following spring. For reproduction, this made sense, as it occured only once per year. However, for the other processes such as mortality, this may appear unrealistic as they could occur at any time of the year. However, it was already difficult to have an annual estimate of mortality for each age class. [187] used a monthly-based IBM for grey wolves but fitted the monthly survival rates to data on 145 GPS/VHF-collared animals[3] in Scandinavia. Considering we were focused on wolves from the Alpine region, and that the implementation of the lesser-known processes was already difficult on a yearly basis, we decided to adjust the model on an annual cycle.

3: They could follow the movements of wolves and therefore easily know if they were dead.

The succession of processes in a cycle is shown in Figure 1.4. First, the cycle started with **reproduction**, followed immediately by the **aging** for all individuals, now old of one more year. This way, pups had the age of 1, meaning it was their first year of life. Because in the wild a lot of pups die soon after they are born, we placed the **mortality** process right

after. Because breeders could be killed during the mortality process, we placed **pack dissolution** right after.

For packs which did not dissolve, the lost breeders could be immediately replaced by subordinates. In M1 (Figure 1.4), replacement by subordinates was favoured over replacement by dispersers only for females (following the sex-biased replacement assumption). Therefore, the **replacement of lost breeding females by subordinates** followed the pack dissolution process in M1.

Thereafter, we placed **dispersal**, and logically **immigration and emigration** which were the direct consequences of the dispersal process. All the processes resulting from dispersal then occurred: integration of dispersers in existing packs as subordinates (**adoption**) or as breeders (**replacement of breeders by dispersers**). The creation of new territories arrived then after in this order: **in pairs of dispersers**, with a subordinate (**budding**), then **alone**.

In M1, the **replacement of breeding males by subordinates** arrived at the end of the cycle to ensure that the replacement of lost male breeders were done first by male dispersers before the male subordinates (following the sex-biased replacement assumption).

In M2 and M3, the processes involving the replacement of breeders were placed differently (Figure 1.5): replacement by both female and male subordinates arrived before the replacement by dispersers in M2 or the opposite in M3. The rest of the process layout was unchanged.

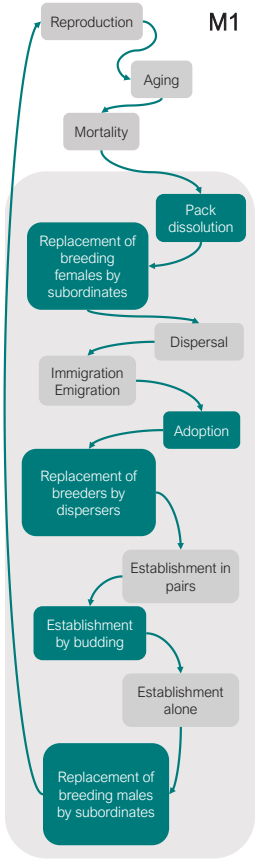

Figure 1.4: The cycle of the IBM for version M1 (only female subordinates were favoured over dispersers to replace breeders). The green boxes were the lesser-known processes. Credits: O. Grente

The circle of life

The IBM was designed as a cycle, repeated multiple times. Each cycle was designed to represent one year, from spring to spring, and started with the reproduction process. All the individuals of the population successively moved from one process to another. Each process was represented once during the cycle. Not all individuals were affected by a process, it was depending on their characteristics.

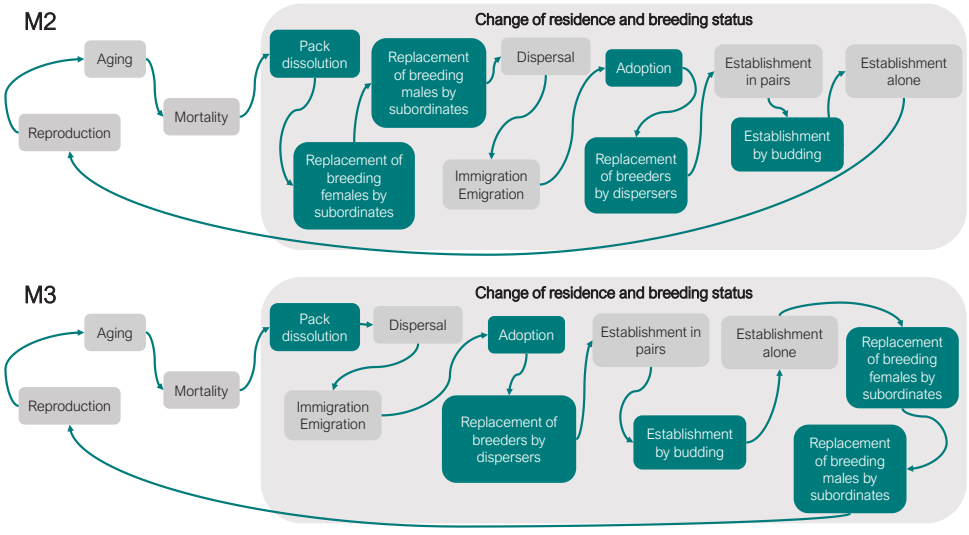

Figure 1.5: The cycle of the IBM for version M2 (top) and version M3 (bottom) where subordinates were favoured over dispersers to replace lost breeders (M2) or the opposite (M3). The green boxes were lesser-known processes. Credits: O. Grente

Launch the IBM

To launch the simulations, we needed to initiate the model with a fictive population and to settle the carrying capacity (*i.e.* the maximum number of packs that could be created in the fictive area we modelled).

There was no accurate information on the composition on packs in France. Therefore, we did not try to copy the French population for the initial fictive population. Instead, we decided to start with a small population which had not reached a carrying capacity, in order to observe how the population behaved during a colonisation phase.

We set the carrying capacity at 30 packs. The number of packs in France is still currently increasing each year and is not stabilising, so it was difficult for us to choose a pack number representative of the situation in France. We intentionally chose what could appear as a limited number of packs (30) compared to what is observed currently in the French Alpine Arc (106 [29]). First, we thought that 30 packs at most would be enough to observe the different effects of the tested lesser-known processes on the wolf population dynamic. Second, it decreased the simulation duration required for the population to reach the carrying capacity (*i.e.* completed colonisation).

We initiated the population with 10 packs and 43 individuals including 5 dispersers. The details of the constitution of each pack is represented in Figure 1.6. We set the annual immigration of 0, 1 or 2 external wolves and the annual emigration to 10% of the dispersers.

We chose to set the age of sexual maturity for wolves in their 3rd year of life (2 years old), therefore excluding pup (1st year of life) or subadult (2nd year of life). This meant that only adults could form a breeding pair. This was consistent with [179] where the earliest age of reproduction of 134 wolves was 2 years old (therefore in their 3rd year of life) apart a very few exceptions of breeding wolves of 1 year old. The studied population in [179] was recolonising Scandinavia, and its density varied greatly across the study period. Therefore, this study encompassed different situations of breeding opportunities, that could be reduced at the beginning of the colonisation (lack of wolves), then could increase with wolf density, to finally decrease at the saturation of the area (all territories are occupied by breeding pairs). Thus, the large temporal collection of age at first reproduction in [179] did represent sexual maturity and not only breeding opportunities.

We ran the model over 25 time steps (*i.e.* cycles). We replicated each scenario 200 times. Therefore, for 81 scenarios, there were $81 \times 200 = 16200$ simulations in total.

The model was launched in R 3.5.2 [193]. We used the R package *NetLogoR* to implement the IBM [194] and the package *pedantics* [195] to calculate the relatedness between individuals using their mother and father IDs. We used the package *SciViews* [196] for the logarithms functions and the package *testthat* [197] to implement tests in our model and to verify the outcomes of the submodels. The R files to run the model are available in the GitHub repository of Sarah Bauduin, under the GNU General Public License v3.0.

[193]: R Core Team (2020), *R: A Language and Environment for Statistical Computing*

[194]: Bauduin et al. (2019), 'NetLogoR'

[195]: Morrissey (2018), *Pedantics: Functions to Facilitate Power and Sensitivity Analyses for Genetic Studies of Natural Populations*

[196]: Grosjean (2020), *SciViews-R*

[197]: Wickham (2011), 'Testthat: Get Started with Testing'

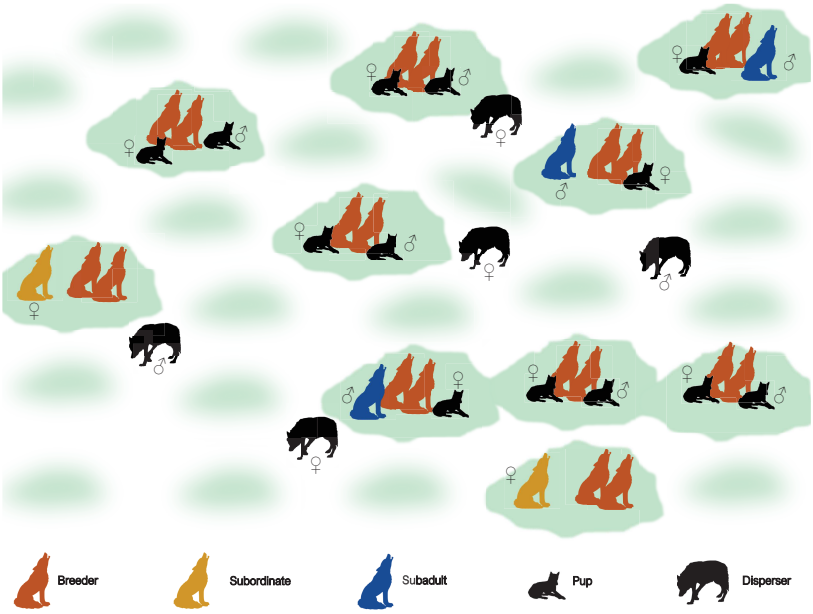

Figure 1.6: The initial population of the IBM with 10 packs and 43 individuals. The spatial representation of the wolf territories (green circles) was only for the purpose of visualisation, as the IBM was not spatial. A breeding pair was always formed by a female and a male. For the other individuals, sex was indicated. Pups were all the wolves in their 1st year of life, and subadults were wolves in their 2nd year of life. All the breeders, subordinates and dispersers in the initial population were respectively in their 5th, 3rd and 2nd year of life. Credits: O. Grente

Press start

We launched the IBM with 10 packs and 43 individuals, and limited the modelled area to 30 territories that can be occupied by wolves. The model for each scenario and each replication ran over 25 times steps (*i.e.* years). There was a total 81 scenarios, 200 replicates for each scenario, therefore totalling 16 200 simulations.

1.4 Result synthesis

Colonisation dynamic

The simulated populations of all our scenarios in our IBM all started with 10 packs and reached 30 reproductive packs (*i.e.* carrying capacity) after on average of 9.8 years (sd = 2.8). In France, the population reached 10 observed packs at the end of 2003 and 30 observed packs at the end of 2014, therefore in 12 years (Figure 1.7). This is therefore consistent with the growth observed in our IBMs. However, despite this consistency, the colonisation dynamic in our simulations and in the French wolf population were different (Figure 1.7). The growth of the observed population was exponential, when the growth of the simulated population was logistic. This is due to the fact that the carrying capacity of our simulated population was low, whereas the French population has currently still not reached the carrying capacity.

There was also an important difference between our simulated population and the population observed in France: the proportion of dispersers in both populations. In France, the number of genetically identified wolves at the end of 2003 was close to 40 [198], but the estimated size through mark-recapture model was around 100 individuals [29]. The difference between the observed and estimated population sizes in France could be explained by the presence of a large number of dispersers in the population, dispersers being less easily detected than residents

[198]: Loup-Lynx (2015), 'Bilan Du Suivi Hivernal 2014/2015'

[29]: Réseau Loup-Lynx (2021), *Bilan de suivi hivernal de la population de loups - Hiver 2020/2021*

[116]. In our IBM, the initial population of 43 individuals included only 5 dispersers (12% of the population). The 12% simulated proportion is consistent with the generally estimated 10–20% of dispersers in a stable wolf population [192]. However, our initial population was a colonising population, therefore in growth and not stable. We should have included a higher initial proportion of dispersers. In Chapter 2 the ratio of resident/disperser will therefore be corrected.

[116]: Cubaynes et al. (2010), 'Importance of Accounting for Detection Heterogeneity When Estimating Abundance: The Case of French Wolves'

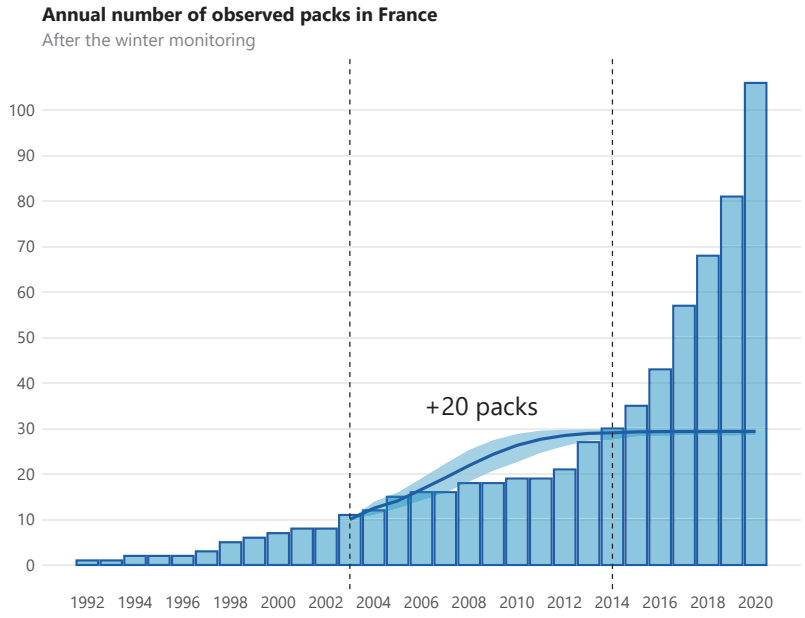

Figure 1.7: Annual number of packs observed at the end of the winter monitoring in France (bars). A pack corresponds to at least 3 individuals, or an attested reproduction the summer before the winter monitoring. Value for year y indicated the result for winter monitoring starting year y. Source: OFB [29]. The blue line represented the annual number of packs simulated in the IBM, first averaged over 200 replications for each scenario, then averaged over the 81 scenarios. The ribbon surrounding the blue line represented the minimum mean and the maximum mean of the annual number of packs for a scenario. Credits: O. Grente

Influences of lesser-known processes

We analysed the influence on the wolf population dynamic that had the four lesser known processes, namely *pack dissolution*, *adoption*, *budding* and *sex-biased replacement of breeders*.

The results of each scenario were averaged over its 200 replicates. We then compared the averaged results of the scenarios for each lesser-known processes. More precisely, we compared the results of the three sets of 27 scenarios, each set having the same parameter value or model version for the given lesser-known process (but each set did not have the same value or version for the three other lesser-known processes). For example, when focusing on pack dissolution, we compared *a)* the 27 scenarios with dissolution parameter 3.1, with *b)* the 27 scenarios with dissolution parameter 4.1 and with *c)* the 27 scenarios with dissolution parameter 5.1, regardless of the parameters of adoption, budding or sex-biased replacement.

Pack dissolution. The higher the dissolution threshold in the model, the higher the number of packs which could dissolve. The three tested parameter values for the pack dissolution (3.1, 4.1 and 5.1) threshold influenced:

- *The total number of simulated individuals*. The number of simulated individuals decreased with the dissolution threshold ($\overline{x}_{3.1} = 189.4$, $\overline{x}_{4.1} = 186.3$, $\overline{x}_{5.1} = 182.8$).

- *The number of packs with a breeding pair at the last year of simulation*. The number of reproductive packs at the 25th time step decreased with the dissolution threshold ($\overline{x}_{3.1} = 29.6$, $\overline{x}_{4.1} = 29.4$, $\overline{x}_{5.1} = 29.2$).
- *The number of new packs formed at the last year of simulation*. The number of new packs formed at the 25th time step decreased with the dissolution threshold ($\overline{x}_{3.1} = 1.3$, $\overline{x}_{4.1} = 2.2$, $\overline{x}_{5.1} = 3.2$).

In short, when pack dissolution was possible for larger packs, this slowed down the population colonisation of the area. It however did not prevent the population to colonise the area, as the three population parameters mentioned were still very close.

Adoption. This process only influenced one parameter of the population structure: *the proportion of residents in the population at the last time step*. This parameter was higher when applying higher adoption probability values, as young dispersers could join more easily existing packs ($\overline{x}_{0.1} = 68.1\%$, $\overline{x}_{0.5} = 69.7\%$, $\overline{x}_{0.9} = 71.2\%$).

Budding. The different parameter values for the budding probability influenced:

- *The time step at which populations reached carrying capacity*. The time for colonisation of the 30 territories decreased with the budding probability ($\overline{x}_{0.1} = 11.8$, $\overline{x}_{0.5} = 9.6$, $\overline{x}_{0.9} = 8.2$).
- *The number of packs with a breeding pair at the last year of simulation*. The number of reproductive packs at the 25th time step increased with the budding probability ($\overline{x}_{0.1} = 29.0$, $\overline{x}_{0.5} = 29.4$, $\overline{x}_{0.9} = 29.7$).

In short, allowing budding more intensely in the IBM speeded up the colonisation of the area because it increased the breeding opportunities.

Sex-biased replacement of breeders. The different model versions for the sex-biased replacement of breeders influenced:

- *The proportion of residents in the population at the last time step*. Favouring the replacement by subordinates for both sexes (M2) provided the lowest proportion of residents in the population at the 25th time step. M1 provided similar results than M3 ($\overline{x}_{M1} = 70.3\%$, $\overline{x}_{M2} = 67.5\%$, $\overline{x}_{M3} = 71.2\%$).
- *The relatedness within breeding pairs at the last time step*. The relatedness was much higher in M2 compared to M1 and M3 ($\overline{x}_{M1} = 0.06$, $\overline{x}_{M2} = 0.26$, $\overline{x}_{M3} = 0.06$).

In short, the assumption of the sex-biased replacement of breeders (M1) provided similar results to the situation when all breeders were replaced in priority by dispersers (M3). This result meant that if the replacement by dispersers was favoured for at least one sex (here males), then the mixing of individuals between packs was ensured.

The key messages of the results

The IBM we modelled provided a dynamic of colonisation different to what was observed in France. This resulted from a low carrying capacity we settled for the modelled population and a low proportion of dispersers in the initial modelled population.

Pack dissolution and budding affected the speed of the colonisation, by decreasing and increasing it, respectively. Increasing adoption possibilities or favouring the replacement of breeders by dispersers, even only for males, increased the proportion of residents in the population (and therefore decreased the number of dispersers). All these results were consistent with our expectations.

1.5 Discussion

We modelled the IBM with population parameters from different studies, mostly from Italy (Table 1.1). It is difficult to compare the structure of our simulated population to observed populations for two reasons. First, the observations in the wild are generally done over several years, therefore we generally do not have the annual representation of the population (*e.g.* [190], [137]). Second and more importantly, in monitoring, there is always a bias linked to sampling, that does not exist in our IBM as our population has no secret for us.

[137]: Fabbri et al. (2018), 'From Predation to Management'

Because it is difficult to compare our simulated population with observed ones, it is difficult to evaluate if our model behaved realistically. We believe the implementation of the four lesser-known parameters, never done before, was important to better mimic the wolf population dynamic. To better analyse that statement, we could have compared our IBM to other IBMs on wolves that have been published [161, 185, 187]. However, we have not just implemented the four processes in a previously published IBM, but we have built our own IBM. This complicated the comparison, as the differences observed between our study and the other sutdies could be due to other parameters or to other processes than the four lesser-known processes we included. Nevertheless, we should have done a 'M0' version of our model where none of the four lesser-known processes would have been included in order to better evaluate the influences of theses processes in our model.

The difference between the parameters or versions tested for these four lesser-known processes was noticeable but moderate. This is a good thing because for the next part of the study, when we will incorporate the depredation and culling components to the IBM, we will have to choose between the parameters or versions for the lesser-known processes. If the choice of a parameter had a too important impact on the wolf dynamic, this could lead us to wrong conclusions in the second chapter, if this parameter was not the right choice.

The integration of these four lesser-known processes will facilitate the study on the culling effects in Chapter 2. Assumption 2 ('*The lethal removals increase the level of depredation*') mentioned in the thesis introduction is mostly based on pack dissolution. The other processes are not directly mentioned in any of the two assumptions about the effect of

lethal removals. It was however necessary to also include all the other processes because they could interact with the effects of pack dissolution. Thus, budding and adoption facilitate the integration of dispersers (potentially produced by pack dissolution), whereas the sex-biased replacement of breeders decreases the likelihood of female dispersers in the population.

Room for improvements. The IBM could have be improved in many ways. First, the non-spatiality is obviously the main limiting factor here. For the needs of the study, a non-spatial IBM was however perfectly fine if not a better choice for many reasons already explained in section *To be spatial or not to be spatial?*. In the case where other scientists would like to use our IBM for other modelling needs about the grey wolves, the non-spatiality of the IBM can however create difficulties.

Second, there are room for improvements in the lesser-known processes. For example, pack dissolution was only possible for packs above a certain size. A decreasing probabilities with pack size could also be a good alternative. However, there is a need for more field studies to evaluate the phenomenon of pack dissolution in the wild, in order to provide reliable parameters for modelling. Similarly, we modelled that males were favoured during the adoption process over females, following what was reviewed in [31]. However, this observation could result from the fact that males could disperse more and farther than females, especially if the sex-biased replacement assumption is true. Therefore, the sex-biased parameter for adoption could be pointless to include in our model if the sex-biased replacement is integrated at the same time.

Finally, I believe the model would have deserved to include the three last processes that were not included in other IBMs: multiple breeding, density-dependent pack size and pack splitting. This would have completed the wolf population dynamic as we know it to-date. We decided to let them aside to decrease the model complexity but above all because these processes are thought to be anecdotal in the Alpine region given the low pack size that is generally observed. With hindsight however, I think it would have been interesting to incorporate them because the density of the French wolf population in the Alpine Arc is increasing and is probably not far from saturation. Integrating biological processes occurring in a saturated population would have been relevant for the management of depredation in this region.

1.6 Conclusion

Chapter 1: The wolf population dynamics

The mission of Chapter 1 is fulfilled. **We simulated a wolf population and integrated most of the grey wolf biological mechanisms** that make the study of its population structure so complex. Among the newly integrated processes, pack dissolution was essential to study the effect of lethal removal, especially regarding Assumption 2. Yet, it had never been integrated in any population model on grey wolves before, to our knowledge. Other lesser-known processes, adoption, budding, and the sex-biased replacement of missing breeders were included as they can modify the population dynamic and structure. Because there is a lack of knowledge regarding the lesser-known processes, we tested different parameter values or versions to model these processes. In the future, more field studies are required to improve quantitative knowledge about these phenomenons in the wild.

We let aside the possibility for multiple breeding, density-dependent pack size and pack splitting to occur in the modelled population. I believe the next step for improving our research in the future would be to include these processes in the IBM or in any IBM on grey wolves, especially when considering the study on lethal removal effects on wolf population dynamic.

Chapter Two

The depredation behaviour 2

Preamble - If Mufassa was a lone wolf

A male wolf was living alone since several years within his territory that he established near the military zone of Canjuers, in the french region of Var. Flocks were already present in the vicinity, but the area was spared from depredations. One day, his skull was found in the bottom of a well. The wolf has been presumably poached. Other wolves took quickly advantage of his death to colonise the vacant territory. From that moment, depredations on sheep by wolves in this area have begun. Today, Canjuers is one of the main hotspots of depredations in France.[a]

[a] pers. com. Christophe Duchamp OFB

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2.1 Aim of the chapter

In this second chapter, we will directly pursue the work initiated in Chapter 1. In the latter, we tempted to model as accurately as possible the structure and functioning of a central-south European wolf *Canis lupus* population.

We now need to understand the depredation behaviour of wolves, in order to implement the depredation component to the previous model. When studying depredation behaviour, a question that is often raised is: *which among the environment or the predator, determines the most the depredation pattern?* This question can be broken down into two separate questions: (1) are some wolves pre-determined to attack more than others (during their whole life or only during certain phases of their lives), no matter the environment? Or, on the contrary, (2) is there a particular set of environmental conditions (including pastoral conditions) which explains the most the frequency of depredations? These are burning questions because they polarise the debate. According to which questions you answer yes, it is tempting to stipulate that their are some *problem wolves* or some *problem pastures/flocks*. This type of reasoning orientates the management towards the elimination of the aforementioned *problem wolves* or *problem flocks*. This basically means making the *pro-farming* or the *pro-wolf* camp satisfied, and the other one dissatisfied.

Answering question (1) is not easy, whether for the grey wolf or other large predators [101]. There are more studies focusing on question (2), such as [55, 199, 200]. One could wonder why such a difference and cynically think that the *pro-wolf* camp has more fans within the scientific community, especially among ecologists. Even if such a judgement would be hardly refutable, there is more. It is simply easier to collect data on abiotic environment or on pastoral practices than on wolves. Not only do you have to know where wolves and packs are (which causes by itself a lot of troubles to field scientists), but also some of their intrinsic characteristics (*e.g.* sex, age, status...) and finally which wolf depredates and how often. Needless to say it is much easier to collect data on the

[101]: Linnell et al. (1999), 'Large Carnivores That Kill Livestock: Do "Problem Individuals" Really Exist?'

[55]: Bradley et al. (2005), 'Assessing Factors Related to Wolf Depredation of Cattle in Fenced Pastures in Montana and Idaho'

[199]: Torretta et al. (2018), 'Wolf Predation on Wild Ungulates'

[200]: Treves et al. (2004), 'Predicting Human-Carnivore Conflict'

number of livestock protection dogs per flock or the forest cover of an area, whether you are part of a camp or the other.

Apart from the problem to eclipse question (1) and what could be keys to understanding the depredation pattern, focusing on question (2) has another major issue. Environmental or even pastoral characteristics are generally strictly context-dependent. In other words, they are hardly transposable from an area to another. For example, [64] showed in Greece that the bigger the flock, the higher the depredation level, whereas in France, medium-sized flocks in the Queyras National Park showed a significant higher level of depredations compared to small or large flocks [201]. This could be linked to environmental differences in both study areas, but also to pastoral components. [64] suggested that their results could be explained by the decline in the quality of protective measures with flock size, whereas the French governmental subsidies of protective measures are adapted to flock size [202]. Even in the same country, results from studies on question (2) can be difficult to apply to other areas than the ones prospected. In France, there are not a unique context of depredations, but many, with diverse environmental or pastoral characteristics, including climates, wild prey species, human density, flock size, periods of grazing, etc... [72]

[64]: Iliopoulos et al. (2009), 'Wolf Depredation on Livestock in Central Greece'

[201]: Plisson (2011), *Etude de la vulnérabilité des troupeaux ovins à la prédation du loup dans le Parc Naturel Régional du Queyras*

[202]: DRAAF (2020), *Instruction technique sur les modalités d'application des mesures de protection des troupeaux contre la prédation*

[72]: Rossi et al. (2012), *Les moyens de protection des troupeaux domestiques contre le loup dans les nouveaux contextes de prédation*

Some could argue that answering question (1) would not provide more management solutions than the answers of question (2), if not less. Indeed, if one can easily act on pastoralism, or even try to manage some environmental characteristics, it is much more difficult to act on the wolves themselves, except for radical options (*e.g.* extirp all wolves from certain areas as in Scandinavia [203]). Let's imagine that young wolves attack more livestock than old wolves, how concretely this could help managers to promote coexistence between farmers and wolves?

[203]: Wikenros et al. (2020), 'Impact of a Recolonizing, Cross-Border Carnivore Population on Ungulate Harvest in Scandinavia'

The argument is conceivable. However, when someone is interested by the effects of culling, especially selective culling such as the one applied in France, this question is not as insignificant as it seems to be for management. As said previously, two polarised visions for the effects of culling are currently confronting [133]:

[133]: Treves et al. (2019), 'Predator Control Needs a Standard of Unbiased Randomized Experiments With Cross-Over Design'

Assumption 1 *Lethal removal is decreasing the depredation level by:*

- *Decreasing predator population size [133],*
- *Threatening survivors, selecting those less likely to depredate [71].*

Assumption 2 *Lethal removal is increasing the depredation level by:*

- *Favouring multiple breeding [133],*
- *Dislocating packs [52].*

This is where studying question (1) can play its full role. There are two possible outcomes: yes, some individual or pack characteristics push certain wolves into depredation, or no, depredation is only the result of a total opportunistic behaviour in combination with environmental or pastoral conditions. In both cases, it gives valuable information on the possible effect of culling. Let's suppose that young wolves are indeed the ones more likely to depredate. Selectively killing those young wolves

would therefore not lead to their pack dislocations, as this phenomenon is mostly linked to breeder deaths [174]. In this case, the second vision of the effect of culling would be compromised. Then, let's suppose that depredation is not linked to any particular wolf's variables: depredation is only the reflect of an opportunistic behaviour. In this case, culling would be random; the risk to cull a breeder would be roughly equal to the rate of breeder occurrence in the population, and dislocation risks would not exceed this rate.

[174]: Brainerd et al. (2008), 'The Effects of Breeder Loss on Wolves'

Finally, to my point of view, the wolf component constitutes the first and most basic level to the depredation pattern, as it is the predator which triggers the attack on livestock. The environment in which the wolf is can only alter this behaviour. It acts as a filter: will the environment enhance the depredation behaviour or reduce it? Contrary to question (2), answers to question (1) would provide the fundamental understanding of depredation behaviour that is currently lacking. This gap in our knowledge explains why visions on the effects of culling can be totally opposed even when considering the exact same environmental and pastoral context [204]. This is why understanding the depredation behaviour should focus on the predator first before the potential environmental alterations, especially when it is a group-living species as wolves. We should also take advantage of the ubiquity of the grey wolf (*Canis lupus*), one of the few large carnivore species to be present across a large part of the globe. In short, answers to question (1) are less likely to be context-dependent than those of question (2).

[204]: Goldfarb (2016), 'No Proof That Predator Culls Save Livestock, Study Claims'

This brings us to focus this chapter on question (1). **Why, in the same environmental-pastoral context, some wolves depredate when others don't? Is it linked to the characteristics of the wolf or of its pack**? We therefore implemented in our individual-based model from Chapter 1 the observations or demonstrations of the depredation behaviour from the scientific or grey litterature, mostly as scenarios. We then implemented a theoretical culling component to the model and tested two different basic management policies. Thus, the whole schematic functioning of the depredation management by culling (*cfr.* Figure 2.1) is integrally modelled. To focus on question (1), the main assumption of the model is that the wolf population evolves in a unique environmental and pastoral context.

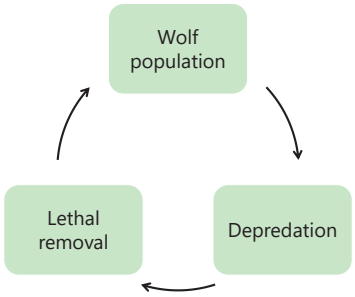

Figure 2.1: Schematic functioning of wolf depredation management by culling. Credits: O. Grente

To sum up

The main aim of this chapter is to test different configurations in which some wolves are more likely to depredate than others because of their individual or pack characteristics only, and to observe the effects of two basic culling policies in the context of these configurations.

2.2 Literature review

Approach

Several degrees of knowledge regarding the depredation behaviour at the wolf level (*i.e. answering question (1)*) are possible. The most robust type of knowledge is coming from scientific articles, in which observations

are used for statistical demonstration. Results can still be biased due to flaw methodology, or they can be inaccurate due to low quality data. These studies are generally reflecting a very local situation, meta-analysis still being rare and methodologically challenging (mainly because a standardised protocol is difficult at large scales). However, the peer-review processing and replications of scientific demonstrations with the same or different datasets decrease these risks and lead to high quality knowledge.

The number of scientific articles available on the theme of question (1) was however limited. We counted less than twenty scientific articles across the world which provide partial answer to this question. More often, these studies did not focus their research on this sole question, and only a minor part of their results could be linked to the depredation pattern at the wolf level. We therefore extended the research of information concerning the depredation behaviour and how it could be linked to wolf individual or pack characteristics. Two strategies were used.

First, we extended the literature review to the more general theme of predation behaviour of wolves. The depredation behaviour of wolves is only a type of predation directed towards livestock instead of wild preys. We can expect that all or part of mechanisms triggering depredation are substantially equivalent to those triggering predation. Investigating how wolves hunt wild preys can then help us to understand the depredation behaviour at the wolf level. Moreover, it can provide valuable insights to understand the potential effects of culling, predation and depredation being intertwined. The identification of the similarities and differences in the predation and depredation behaviours can indeed allow us to explore the mechanisms involved in the two visions of the effects of culling. The first vision hypothesised that culling selects individuals less likely to depredate, in other words more likely to predate wild preys. The second vision hypothesised that culling, by causing the isolation of individuals from their packs, prevents typical group hunting strategies on wild prey, forcing individuals to report on livestock.

Second, we extended the literature review to a less robust information, sometimes called 'the grey literature'. This included reports or book chapters which were not published as a scientific article in a journal. They could consist in scientific studies with statistical analyses. However, they were not peer-reviewed. The risks of biased and inaccurate results are therefore stronger than for scientific articles. Keeping this in mind, these reports could still reinforce results from the published papers or open reflection about some aspects that could not be found in the traditional scientific literature.

During my PhD, I also had the opportunity to exchange with a large panel of stakeholders directly concerned by the depredation behaviour of wolves in France and elsewhere. For this chapter, I took benefit from this experience by including in my literature review the observations and the experiences of these different stakeholders. First, I had access to operations reports of the *governmental agents* who were deployed in pastures facing high levels of depredations in order to cull the wolves in depredation phase. They were equipped with thermal cameras and provided basic information about the wolves' approach of flocks. I also included the works of two organisation which are closely linked to the

depredation behaviour of wolves in France, and with whom I exchanged on several occasions throughout my PhD. The first organisation, *Institut pour la Promotion et la Recherche sur les Animaux de protection (IPRA)*, produced reports of field observations of wolf-livestock interactions but also of wolf activities aside from depredations, through thermal cameras within the context of its 'CanOvis' project. The second organisation, *Centre d'Etudes et de Réalisations Pastorales Alpes-Méditerranée (CERPAM)*, produced reports concerning recommendations about the implementation of livestock protective measures. These reports generally did not contain direct observations of depredation, but included information about the depredation contexts and the wolf hunt strategies inferred *a posteriori* of the depredation events, mostly through field visits and interviews with farmers. I also had direct exchanges with two French farmers, Sylvain Rigeade from GAEC Brin de Paille, who lives in an area of high depredation level in France and deployed a system of camera-traps in the vicinity of his area in order to follow wolf's but also wild prey's movements. He contacted me to exchange about his observations and the reasoning he developed based on them. The second farmer, also a shepherd, is Henri Cotton, whose flock has been attacked repeatedly by wolves, mainly in the Jabron valley in Alpes-de-Haute-Provence, for several years now. I had also the opportunity to talk to Thierry Escallier, a lieutenant from the 'louveterie' which is a special section of unpaid hunters named by the French authorities to cull wolves in the most attacked farms. Finally, I had short exchanges by emails with the biologist Ilka Reinhardt from the LUPUS German Institute of Wolf monitoring and research who provided insights about the depredation behaviour of wolves in Germany.

I found deeply stimulating to collect all these experiences from a large diversity of stakeholders who have different affinities with the *Canis lupus* species and the wolf depredations. I took special care to include as many types of stakeholders as I could, given the opportunities I had during my PhD. I kept in mind that their personal points of views on the wolf depredation subject could impact their perceptions of their observations. Nonetheless, I believe that the plurality of their voices and experiences would provide valuable insights or assumptions to test during this chapter, but also additional material to interpret results throughout the whole PhD.

I organised the literature review into two main parts: first, the predation behaviour on wild prey, and second, the depredation behaviour.

Hunting groups

The most remarkable feature of *Canis lupus*, as we have seen in Chapter 1, is the social organisation of its individuals in packs. This organisation makes the study of the depredation behaviour more complex, as there are many possibilities regarding hunting strategies in a pack. Contrary to solitary predators, solitary hunting is not the only option for wolves in packs. They can also hunt with the whole pack or with only a fraction of their pack [31]. In the last case, questions can be raised concerning the type of individual associations to form hunting groups within a pack: *are the breeders on one side, and the subordinate on the other side? are hunting groups formed by mixed associations of individuals of all ages and statuses?*

[31]: Mech et al. (2003), *Wolves: Behavior, Ecology, and Conservation*

Again, these raised questions can appear of relatively minor importance for managers and of interest only for curious biologists. However, the answers to these questions can strongly impact the two hypotheses of the effects of culling. To give some examples, if wolves are completely able to hunt wild preys alone in an area, it is less likely that pack dislocation would lead to a massive report of predation on livestock. If breeders rarely hunt with their offspring, this also challenges the second hypothesis which generally considers the predation (including depredation) as a learned behaviour.

If you ask someone from the general public about wolf hunting strategies, this person will generally picture a large pack of wolves, probably hunting bisons *Bison bison* or elk *Alces alces* in snow, in a highly coordinated strategy led by an 'alpha' wolf. This widespread point of view finds its roots in TV documentaries shot in the wilderness of North America, with a large touch of fiction to depict its fluffy protagonists. What's wrong with this picture? First, the diversity of wild prey in the wolf distribution is very large, and this type of hunting (*i.e.* chasing herds of very large ungulates in open areas) only represents a small fraction of what is found worldwide for *Canis lupus*. Besides, the general public would be very surprised that the use of cooperation in hunting is still debated among the wolf biologists. [205] compiled the scientific knowledge, field observations of wolf pack hunting and wolf biologists beliefs; they concluded that there is more evidence of 'simple and straightforward' collective hunts than cooperative strategic hunts for packs. In a complete different approach, [206] modelled wolf-pack hunting strategies from two simple movement rules identical for all wolves of a pack, where no hierarchy or no communication were required. Therefore, the need for a leader, potentially a breeder, to have a successful hunt for a pack does not appear necessary.

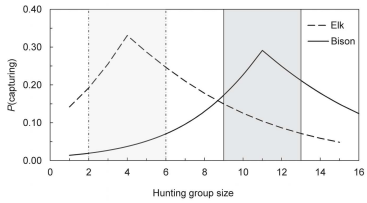

Figure 2.2: Comparative effects of group size on the success of wolves capturing bison and red deer. Adapted from MacNulty *et al.*, 2014.

[205]: Peterson et al. (2003), 'The Wolf as a Carnivore'

[206]: Muro et al. (2011), 'Wolf-Pack (Canis Lupus) Hunting Strategies Emerge from Simple Rules in Computational Simulations'

This leads us to the next question: if there is no need for a leader or a fancy coordination between individuals, why wolves need to be in groups to hunt? There could be two reasons. The first reason would be a better efficiency to seize large prey. This has been demonstrated in the Yellowstone National Park (YNP) [207] and in Scandinavia [208]. The second reason would be a better efficiency to defend the carcasses against other wolves or predators. To my knowledge, this reason has only been suggested by [158, 208, 209].

[207]: MacNulty et al. (2014), 'Influence of Group Size on the Success of Wolves Hunting Bison'

[158]: Ausband et al. (2021), 'The Effect of Group Size on Reproduction in Cooperatively Breeding Gray Wolves Depends on Density'
[208]: Sand et al. (2016), 'Prey Selection of Scandinavian Wolves'
[209]: Jedrzejewski et al. (2002), 'Kill Rates and Predation by Wolves on Ungulate Populations in Bialowieza Primeval Forest (Poland)'

Size of hunting groups

So, the larger the better? Not exactly. [207] showed that the success of capture of bison (*Bison bison*) peaked between 9-13 wolves and between 2-6 wolves for red deer (*Cervus elaphus*), meaning performance was decreasing beyond (*cfr.* Figure 2.2). This phenomenon was apparently not linked to the fact that larger groups inevitably included individuals which have not the best hunter profiles (*i.e.* inexperienced or ageing wolves) or collisions between individuals, but would result from a less intense engagement from individuals [210]. In other words, the more they are in a group, the less they could feel involved, probably hoping others would do the job at their place [1].

[210]: MacNulty et al. (2012), 'Nonlinear Effects of Group Size on the Success of Wolves Hunting Elk'

1: The same principle may apply to emails with a large number of recipients.

In addition, the larger the hunting group, the higher the number of mouths to feed, the less food intake per individual [211]. Consequently, hunting group size is a compromise between hunting efficiency or protection of carcasses on one side and share of food on the other side. This compromise actively depends on the size of the biggest and commonly available preys. Large prey as bison will favour large hunting group, because the group will be able to kill it and the catch will provide a large amount of food. More modest prey as red deer would still favour hunting group rather than solitary hunting, but would not support the food requirements of a large group, therefore limiting hunting group sizes [209].

[211]: Metz et al. (2011), 'Effect of Sociality and Season on Gray Wolf (Canis Lupus) Foraging Behavior'

Up to now, we only talked about hunting groups but not total pack size. The latter compromise also applied to pack size. There are two possibilities. First, the pack hunts as a unique hunting group, as in [208], because the pack is optimal in size to hunt and to protect the catch. Second, the pack splits into two or more hunting groups. In Poland [209] or in the YNP [211], the larger the pack, the more frequent the splitting into hunting groups. In the Polish studied forest, it was apparently more optimal for packs to form hunting groups of 4 wolves (*cfr.* Figure 2.3), the calf red deer being the most hunted prey. European bison *Bison bonasus* was yet available (5.6%), but less than the red deer (35.4%). Bison hunting was probably not sustainable enough to maintain large hunting groups because of its low density (or for other reasons, the studied area being rather small and made by closed forests, preventing the form of bison hunting used in open area).

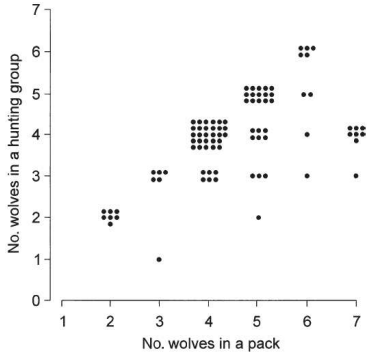

Figure 2.3: Wolf hunting group size compared to pack size in Bialowieza Primeval Forest, Poland. From Jedrzejewski *et al.*, 2002.

All of this explains why pack size tend to narrow around a medium value in a given population. However, smaller or larger packs can still occur (because of a high number of mortality events or low number of dispersal events, respectively). In this case, these packs adapt their diet. In Scandinavia, [208] found that pairs of individuals fed more on roe deer (*Capreolus capreolus*), when packs of at least three individuals favoured elk (*Alces alces*) over roe deer. Wolves are also able to actively modify their hunting target according to their situation. This has been documented for a breeding female wolf in Scandinavia which switches her diet from elk to roe deer when she lost all the members of her pack and ended on her own [212].

[212]: Sand et al. (2006), 'Effects of Hunting Group Size, Snow Depth and Age on the Success of Wolves Hunting Moose'

Composition of hunting groups

So far, we talked about hunting group size as if all individuals were equal in terms of hunting abilities. But is it really the case? Some wolves could be more experienced than others, or have better body conditions to effectively hunt and kill prey. [213] observed that wolves were the most efficient to hunt when they were around 3 and 5 years old. Above 5 years old, we could assume that body conditions were responsible of the decrease in hunting efficiency. But below 3 years old, it could be due to a lack of experience or low body conditions, or both. According to [212], it could be both. They showed that the pack success of elk hunting in Scandinavia was depending on breeding male age, with a rapid increase between 1 and 2 years old likely corresponding to body growth, and was still increasing after 2 years old, up to 5 years old, with less intensity, likely corresponding to increase of experience.

[213]: Mech et al. (2015), *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*

Therefore, at equal age, we expect the bigger, the better. This is what [214] showed for red deer hunting success in YNP. However, there was an important subtlety in their results (*cfr.* Figure 2.4). Large wolf body size was above all an advantage during the killing phase of red deer hunting. It appears less crucial for launching the attack on herd, and even slightly unfavourable when selectively targeting one prey from the herd. Because females generally weigh less than males, they tend to be less efficient to kill large prey as red deer than males [214], but not during the previous phases of chasing herd or isolated prey [214, 215]. Therefore, for a given age, we can expect females as efficient as males to hunt small prey as roe deer, including during the killing phase.

[214]: MacNulty et al. (2009), 'Body Size and Predatory Performance in Wolves'

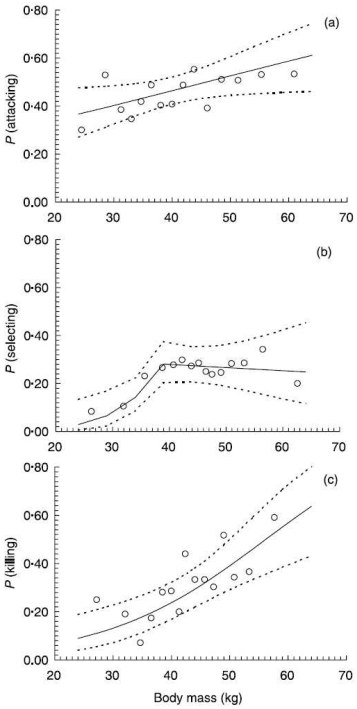

Figure 2.4: Effects of wolf body mass on the probability of individual wolves to attack (a), select (b), and kill (c) red deer (*Cervus elaphus*). Adapted from MacNulty *et al.*, 2009.

[216]: Linnell et al. (1998), 'Timing and Synchrony of Birth in a Hider Species, the Roe Deer Capreolus Capreolus'

Season effect on hunting groups

Once the ecosystem has driven pack size and hunting groups size to the most optimal value given the available set of prey species, one could think the wolf hunting strategy is immutable. If unexpected events as almost simultaneous mortality events happens in a pack, as in the case of the Scandinavian female wolf mentioned earlier [212], one could think that the optimal hunting strategy is only postponed until the pack size returns to its previous optimal state.

However, the wolf group hunting strategy is not immutable, even when considering packs or prey populations without extraordinary events. The main factor to explain variations in wolf hunting strategy within a pack, or for a given wolf, is seasonality. In temperate regions where wolves live, plant resources on which ungulates depend tend to rarefy in winter. Ungulates generally respond by adjusting births to spring, in order to let their offspring grow when resources are plentifully available [216].

In response to prey annual fluctuations, the wolf life cycle is annual, with pup births in spring as prey birth. This annual reproduction and the resulting two annual dispersal events (*cfr.* Chapter 1) affect a lot the composition of packs throughout the year, notably its size and its age structure, but also the whole population with a varying number of lone wolves in dispersal.

Hence, seasonal prey vulnerability and pack composition have different repercussions on the hunting strategies throughout the year. The most striking effect is on **pack cohesiveness** [211]. In winter in the YNP, pack cohesion is at its highest: a wolf is twice as likely to feed on a carcass killed by other members of its pack in winter than in summer [211]. This could appear counter-intuitive as ungulates are weaker in winter due to plant rarefaction [209]. In addition, wolves sink less into deep snow than ungulates, which should give them an advantage during hunt [215]. However, the easiest preys to catch, ungulate calves, are not as vulnerable and numerous as they were during spring. In some cases as in Canada, ungulates can even migrate towards more welcoming areas in winter [217]. In Scandinavia, there was no demonstration that hunting was easier for wolves as winter went by, suggesting ungulates were affected by winter as much as wolves [215]. In Canada, [217] showed that a pack focused its hunting on elk specifically during winter because it was the only ungulate species which did not migrate outside the pack's area.

[215]: Wikenros et al. (2009), 'Wolf Predation on Moose and Roe Deer'

[217]: Huggard (1993), 'Prey Selectivity of Wolves in Banff National Park. I. Prey Species'

Hence, in cases where prey are harder to catch in winter, this can explain why packs tend to be more cohesive during hunting.

In summer, pack cohesiveness is therefore lower [211]. As said previously, this could be related to the profusion of ungulate calves, requiring a lower hunting efficiency for wolves. This may also be related to pup's births. [153] also observed that the feeding of pups fell to breeders, non-breeders apparently being of little help to bring food to the *rendez-vous* site. This suggested that breeders probably spent more time looking for food than non-breeders in a pack, creating splits of huntin groups compared to winter. In his field notebook, [153] observed in 10 *rendez-vous* sites in the French Alps during several years that non-breeders could sometimes go with a breeder, or form hunting subgroups of 2-4 non-breeders, but the whole pack was rarely leaving altogether from the *rendez-vous* site at the same time. Even breeders were generally not leaving together from the site, and even less frequently coming back together. This is partly consistent with what S. Rigeade analysed from its camera-trap system in Drôme (France), where he approximated the location of the den and *rendez-vous* site with the hours and frequency at which wolves were observed by camera-traps. According to his analysis, wolves tended to leave altogether from these sites at the beginning of the night but rarely, if ever, coming back together at dawn. Both observations from [153] and S. Rigeade suggest splits during prey research and hunting in summer.

[153]: IPRA (2020), *Carnets d'observation : la meute sur son site de rendez-vous*

At the end of the summer season, which can extend to fall, the pack energetic need is at its highest: pups have almost their adult size, and the fall dispersal has not yet occurred. [153] observed pups starting to follow the rest of the pack during hunts from October, and the resting sites were progressively abandoned. The cohesiveness is then increasing from this period. However, [211] showed that in winter, pups were almost systematically found with a breeder at a carcass in YNP, but it was less true for subadults. This could be the first signs of oncoming dispersal.

Hunting behaviour

Up to now, we have not said much about how wolves, alone or in group, really 'hunt'. First, *how do wolves search preys?* The exploitation of the territory seems quite methodical.

[218]: Jedrzejewski et al. (2001), 'Daily Movements and Territory Use by Radio-Collared Wolves (Canis Lupus) in Bialowieza Primeval Forest in Poland'

[218] in Poland and [153] in France observed a different tactic from [217]. Wolves used their territory in a cyclic manner, a different part of the territory being used every night. In Canada, Huggard [217] observed that wolves tended to go systematically to locations within their territory where herds of 2-100 red deer predictably gathered in winter. However, they could also opportunistically fall on a smaller and solitary deer species on their way (*e.g.* on the white-tailed deer, *Odocoileus virginianus*). He called these two tactics *'intentional and random encounters'*, respectively.

To travel within their territory, potentially for hunting, wolves facilitated their travels by using tracks [153] (S. Rigeade, pers. com.). This way to describe wolves travelling predefined paths in their territory in search for opportunistic encounters with preys [205] is consistent with the training I received from the French national network in charge of the wolf monitoring in France. Wolves were described during this training as leaving tracks in a straight line, without wandering as dogs, as if *'they*

knew where to go'. I could observe this behaviour myself, when I followed the tracks of a lone wolf in snow between Tarn and Hérault in France: the tracks were straight over 4 kilometres (*cfr.* Figure 2.5).

As the formation of hunting groups, prey research strategy may also change with season.Telemetry results from [219] showed in the French Alps that two breeding females restricted their movements around den and *rendez-vous* site once pups were born in spring. The use of tracks is very noticeable in winter (*cfr.* Figure 2.6) and less in summer.

The second question is: *once they encounter a prey, how do wolves generally attack it?* Wolves are generally not depicted as ambushing predators in the scientific literature [205]. Contrary to lynxes for example, wolves would rely on their running abilities and endurance to exhaust fleeing prey. This means that, in the case where prey are defying wolves and not fleeing as bisons can do, wolves tries to get them run [220]. According to [217], this strategy aimed to split fleeing ungulate herds in order to target the weakest individuals.

However, what happens for preys not living in herds, as elk and roe deer? Observations of [215] in Scandinavia showed wolves hunted elk and roe deer by chasing them, but generally on short distances (a few hundred metres only, not exceeding 2 km). Most elk survived, mainly just by escaping wolf's attacks, but a minority faced wolves (6% of attacked elk) and all of them survived. On the contrary, roe deer did not try to face wolves and relied only on its reactivity to spot wolves and its speed to escape predators. In both cases, this meant wolves had interest to get as close as possible without being detected by prey before launching the attack to get their prey run. Therefore, even if we do not expect wolves to excel at patiently ambushing prey as lynxes, they could be less brutish than we think. For both ungulate, hunting success rate was around 25% [215].

All these observations involved wolves living in areas at high latitude, with frequent snow during winter, large prey and areas generally with low human density and infrastructures. Hunting behaviour in other types of habitat, as Southern Europe, is not as much documented. In France, the first habitat recolonised by wolves is mainly mountainous, steep, open at high altitude, with prey living in herds and outperforming wolves for running in this habitat (chamois *Rupicapra rupicapra*, Alpine ibex *Capra ibex*). Do wolves apply the same strategy of splitting herds without ambushing? French wolves also inhabit more forested areas at lower altitude, less steep or even flat, with prey living in herds as wild boar (*Sus crofa*) or a solitary life as roe deer where we could expect ambushing to be an advantageous hunting strategy.

[219]: Anceau et al. (2015), 'La prédation du loup sur les ongulés sauvages : impacts directs et indirects'



Figure 2.5: Wolf tracks in snow in Courniou, Hérault, France. Credits: O. Grente

[220]: Gray (1987), *The Muskoxen of Polar Bear Pass*

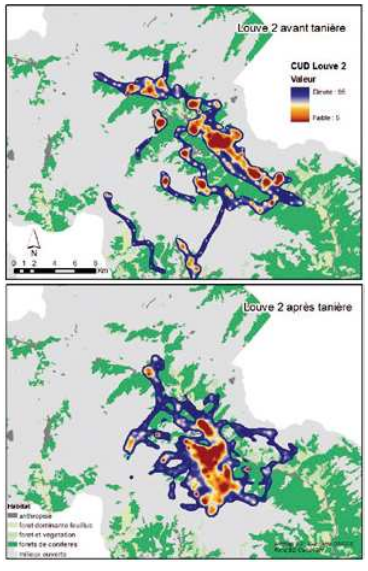

Figure 2.6: Territory use of space based on GPS telemetry data of a breeding female wolf in the French Alps, shortly before pup birth (up) and after pup birth up to August (down). Adapted from Anceau et al., 2015.

Prey selection

Once a wolf or a hunting group encounters a potential prey, it has first to identify the animal as a prey and to decide to launch the attack (both steps being the prey selection) and then to successfully kill it. Prey selection relies on two parameters: encounter rates and prey vulnerability.

The first point is quite easy to catch. The more preys and wolves in the same area, the more encounters between both of them, and the

more opportunities for attempting a catch for wolves. In France, the diet analysis of 5 packs across the French Alps unsurprisingly showed higher consumption of chamois and Alpine ibex for packs at high elevations where these species are easily found, than for packs located at lower elevations [221]. In Canada, [217] showed that wolves used low elevations as red deer, but avoided high elevations where bighorn sheep and mountain goats were more common. Inevitably, this was reflected in the wolf's diet of this study, from where the last two species were almost absent. In Italy, [222] showed great spatial-temporal overlap of wolves with wild boar and roe deer but not with fallow deer (*Dama dama*) and chamois. Consequently, the last two species constituted only a small part of the wolf's diet in this region. In [217, 222], is the spatial overlap with certain preys intentional from wolves? It's hard to say.

[221]: Flühr (2011), *Analyse Spatio-Temporelle Du Régime Alimentaire Du Loup (Canis Lupus) Dans Les Alpes Françaises*

[222]: Torretta et al. (2017), 'Wolves and Wild Ungulates in the Ligurian Alps (Western Italy): Prey Selection and Spatial-Temporal Interactions'

Wolves could also select their preys according to their vulnerability. In YNP, bison was not the favoured prey, even for large packs [207], probably because the injury risks were higher than the other available prey. [217] showed that hunting wolves did not select between ungulate species they encounter (mostly elk and deer) and hypothesised they did so because both species had equivalent vulnerabilities: these ungulates first fled to escape wolves before defending themselves, involving a reduced injury risk. This has also been shown in Scandinavia, with no strong selection between roe deer and elk [208]. A good example of vulnerability is the Mediterranean mouflon (*Ovis gmelini musimon x ovis sp.*) in France. Reintroduced in the Alps for human hunting, it is a species poorly adapted to steep and snowy habitats like the Alps, especially compared to chamois. When wolves recolonised the French Alps, mouflon was the main prey found in their scats [221]. When mouflon density fell in response to wolf predation, the mouflon's part in wolf's diet was mainly reported on roe deer.

There is not only vulnerability differences between species, but also within species, between age classes. In Scandinavia, wolves more successfully caught calf elks than adults [215]. Wolves in the Tuscany region of Italy showed high intake of young wild boars [223]. Remains of adult wild boar and calves of red deer and of roe deer were present in scat contents as expected considering prey abundance, contrary to adult of red and roe deer, with lower rates than expected. Wolves in Poland apparently selected the red deer calf in spring and, as calves were growing and less vulnerable, wolves reported their predation to wild boars, and in particular young wild boars [209]. The other available species were rarely hunted, maybe because they were not vulnerable enough (as bison or elk) for the average wolf hunting groups, or too small to feed the whole hunting group (as roe deer). Therefore, we should not forget that prey selection does not rely only on prey encounters or vulnerability, but also on hunting group size, as we have previously seen.

[223]: Mattioli et al. (2011), 'Prey Selection and Dietary Response by Wolves in a High-Density Multi-Species Ungulate Community'

Nevertheless, for all these studies, it is difficult to know if wolves *actively* selected their prey, by intentionally roaming in their habitat and by directing their hunt towards the most vulnerable species or individuals. The reason is, scientists generally do not know the failed attempts, but only the successful catch, through the carcasses or wolf scat analyses ([208, 217, 221–223]). If a type of prey is selected by wolves but generally not successfully killed, it is absent from these indices, misleading the study conclusions. Despite this, it was possible to consider active selection

of prey as possible. In the case of the wolves in Tuscany [223], young wild boar were highly consumed around 10 months, when they have 50% of their adult weight, whereas the consumption of deer calf seemed more homogeneous during the first months following their birth. This pattern could show that wolves are actively selecting medium-sized young wild boar, and not just the most vulnerable individual (assuming protection by adult wild boar of their offspring does not change until adulthood), in order to maximise food intake by avoiding light newborns, when minimising risk injury by avoiding big adults.

To put wild prey hunting in a nutshell

Around the world, wolves seem to feed on a lot of food sources, from very small animals (rodents, birds...) to very large, and sometimes larger than them (elk, bison). They are also occasional scavengers. But wolves incontestably seem to target living ungulates [224]. The identity of the most eaten ungulate species is very different according to the areas. This could be a reflect of the optimal foraging theory, where a compromise is done between time spent on searching (*i.e.* **encounter rates**) and injury risks when handling a prey (*i.e.* **vulnerability**) on one side, and benefits as **food intake** on the other side. It is hard to know if this optimal choice is conscious (wolves learn what is the best catch) or not (they are fully opportunistic). In addition, the optimal foraging theory does not only apply at the individual level, but also at the pack level, determining pack size but also hunting group size and composition. This theory varies across the year, mostly because of wild prey life cycles.

[224]: Janeiro-Otero et al. (2020), 'Grey Wolf (Canis Lupus) Predation on Livestock in Relation to Prey Availability'

Livestock selection

Now that we have identified the main features of wolf hunting, we can focus on wolf depredation. There is no reason to think depredation would be subject to different selection rules than standard wolf hunting of wild preys. For example, several observations during or after depredation events indicated similar hunting behaviours as described earlier, such as splitting flocks (IPRA, 2018) or attacking an isolated group of individuals (IPRA, 2020, [225]) and making them flee.

[225]: Bonnet et al. (2021), *Diagnostic de vulnérabilité face à la prédation du loup GEAC de la Viste, commune de Curel*

The question we will try to answer in this part is: *why would wolves select livestock over wild prey in some circumstances?* The short answer is: the profitability to kill livestock must exceed the profitability to kill wild prey for this wolf. According to our literature review, profitability can be defined as the balance between benefits (food intake) and costs (encounter rates and vulnerability). So when does this configuration happen, and for which wolves?

Encounter rates

First, selection of livestock over wild prey could be explained by encounter rates. If a wolf encounters as frequently livestock as wild prey, or more, this situation may increase the attempts of this wolf to kill livestock, despite the other predation features (vulnerability and food intake of

both livestock and wild prey). For example, [51] showed in Italy that livestock was more consumed when wild prey were less abundant, because it induced an increasing proportion of encounter rates with livestock. This was a situation that was exacerbated in Greece, where wolves almost exclusively fed on livestock because the density of wild ungulates was low [65].

[51]: Imbert et al. (2016), 'Why Do Wolves Eat Livestock?'

[65]: Petridou et al. (2019), 'Wolf Diet and Livestock Selection in Central Greece'

Other parameters linked to wolves' characteristics could also modify encounter rates between wolves and their preys, whether they are domestic or wild: **the wolf's resident status, reproductive status and its stay duration within a territory**.

Resident status. Encounter rates are primarily defined by the wolf territory location. I see three possibilities. First, the territory is not overlapping any livestock herd, therefore encounter rates are close to zero, as extra-territorial movements are not frequent [226], especially if other wolf territories are in the vicinity. Second, there are at least one herd on the territory, drastically increasing encounter rates compared to the first possibility. Third, the wolf has no territory yet, because it is dispersing. Its rate of encounters with livestock could be high or low, depending on the degree of pastures within its dispersing area.

[226]: Mech (1977), 'Wolf-Pack Buffer Zones as Prey Reservoirs'

Let's consider wolf-livestock encounter rate equal between dispersing and territorial wolves in a densely pastured area. If depredation is only depending on encounter rate, then dispersers and residents should have similar individual depredation rate. At the population level, the rate of depredation according to the resident status should represent the ratio of dispersers and territorial wolves in the population. Dispersing wolves generally do not constitute the major part of a population (*e.g.* ~ 20% in the Western Alps [190]). This means that the depredations would in majority originate from territorial wolves if we only take into account encounter rates.

[190]: Marucco et al. (2009), 'Wolf Survival and Population Trend Using Non-Invasive Capture-Recapture Techniques in the Western Alps'

This simplistic vision is only met once in scientific literature, in Minnesota, USA, [50]. In the rest of the literature, the dispersers could be less likely to depredate than residents, or the opposite. In Central Italy, only one depredation event over 27 (~ 4%) was attributed to a dispersing wolf, whereas dispersers represented 30% of the studied population [137]. On the contrary, livestock were found in higher proportions in the diet of dispersing wolves (35%) compared to wolves in pack (20%) in Liguria, Italy [51]. In Wisconsin, USA, only 62% of the depredation events were attributed to packs [227]. These differences with the simplistic vision stated above can originate from unbalanced encounter rates between dispersers and residents. It could also come from the other features linked to the predation behaviour, vulnerability and food intake, that we will see in the following parts.

[50]: Fritts et al. (1992), *Trends and Management of Wolf-Livestock Conflicts in Minnesota*

[137]: Fabbri et al. (2018), 'From Predation to Management'

[227]: Treves et al. (2002), 'Wolf Depredation on Domestic Animals in Wisconsin, 1976-2000'

Reproduction. Moreover, there is not just one type of resident wolves. Encounter rates can also depend on how residents move within their territory. As we have seen in section *Season effect on hunting groups* on page 64, the movements are directed from and towards the den and the *rendez-vous* site. Therefore, reproduction can modify encounter rates between resident wolves and livestock. As one might expect, proximity to these sites when they are in use by wolves increased the risk of

depredation for pastures [55, 201] [228]. However, this could be more complex than just the distance between pastures and wolf sites. As we have seen, wolves move along tracks. If a pasture is close to a den or a *rendez-vous* site but is not close to the tracks used by wolves, the encounter rates are low. During their observations with thermal cameras of wolves in the French Alps, [153] observed a group of 12 wolves which did not attempt attacks on a flock located at 700 meters from the *rendez-vous* site. This flock being unprotected (no shepherd nor dogs), vulnerability did not seem to explain this lack of interest from wolves.

[228]: Gula (2008), 'Wolf Depredation on Domestic Animals in the Polish Carpathian Mountains'

Yet we have seen that reproduction does not affect all pack members the same way. The breeding male is in charge of finding food when pup are just born in spring and fed by the breeding female which stays in the den. During this short period, its encounter rate with livestock is equal or higher than the breeding female, and potentially than the other members of the pack if any. This might explain, partially or totally, the result from [97] who showed in Minnesota that killing wolf male adults reduced depredation risks more than subadult males or females of any age. However, all the other studies which reviewed or tested this sex-effect did not find significant results [50, 101, 227] [229]. There could be several reasons to that. First, the period where the breeding female is exclusively in the den is very short. Second, flocks as in the French Alps are not always present in pastures at this time of the year. Third, the difficulty to attribute with certainty depredation to individuals may prevent studies to correctly analyse this effect.

[97]: Harper et al. (2008), 'Effectiveness of Lethal, Directed Wolf-Depredation Control in Minnesota'

[229]: Octenjak et al. (2020), 'Wolf Diet and Prey Selection in Croatia'

The period when both breeders are active to feed pups is however longer and extends up to the integration of pups to hunting in fall. If breeders are actually more active than subadults to feed pups [153], then it could imply more moves from breeders to find food, with higher encounter rates with livestock than subadults. Surprisingly, except [97] with the removal of male adult, no other study had showed that there was a difference in the tendency to depredation between breeders or subadults [50] [96]. However, Ilka Reinhard from the *LUPUS German Institute of Wolf monitoring and research* told me that genetic analyses in Germany indicated that damages occurring within wolf territories were probably mostly due to breeders, which is consistent with this hypothesis.

[96]: Bradley et al. (2015), 'Effects of Wolf Removal on Livestock Depredation Recurrence and Wolf Recovery in Montana, Idaho, and Wyoming'

Territory knowledge. There is one last parameter which could influence encounter rates between wolves and livestock. Do you remember the theory of [217] about wolf's movements, *intentional and random encounters*? The intentional encounters would dictate the direction and the tracks wolves are using, because they are targeting food sources (*e.g.* ungulate herds with predictable locations) that they know. To actually know these sources, wolves need to spend time on an area. The sources can be wild prey or livestock. Therefore, time spent on a area could induce less depredations (because wolves know wild prey resources better, as suggested by [51]) or more depredations (because wolves know livestock locations better).

[51] suggested that livestock has high detectability compared to wild ungulates in Italy, therefore a territorial wolf would require less time to learn where to find flocks. Following this reasoning, time spent on a area would above all decreases depredation by increasing encounter

rates with wild prey. To my knowledge, only [230] tested the influence of time spent on a territory on depredation, and only at the pack level. They showed that the number of depredations per pack was positively correlated to the number of years spent on a territory in Wisconsin. If we consider predation only influenced by encounter rates, with livestock much more detectable than wild prey, then this result undermines the assumption of [51]. However, there is no indication about if the number of depredation was analysed per year or not. If yes, the result of [230] then supports the assumption that time spent on an area could favour encounters between livestock and wolves. If no, the positive link could simply reflect the higher rate of encounter rates expected by chance for pack living longer on an area.

[230]: Wydeven et al. (2004), 'Characteristics of Wolf Packs in Wisconsin: Identification of Traits Influencing Depredation'

Vulnerability

It is widely agreed that livestock is very vulnerable to predation, essentially because they lost their anti-predator behaviour during the selection process induced by humans. To decrease vulnerability, farmers can protect their livestock with protective measures (shepherds, dogs, fences...). This is indeed effective, as seen in [231] and [232] in the French Alps, in [64] in Greece, in [89] in the USA and in [224] who reviewed that unprotected flocks worldwide showed the higher rates of depredation. Some farmers noticed that, when they intensified the livestock protection measures following attacks, wolves seemed to report their attacks on a less protected breeding batch or on neighbouring flocks (CERPAM, pers. com.).

[231]: Espuno et al. (2004), 'Heterogeneous Response to Preventive Sheep Husbandry during Wolf Recolonization of the French Alps'

[232]: Landry et al. (2020), 'Interactions between Livestock Guarding Dogs and Wolves in the Southern French Alps'

[89]: Musiani et al. (2003), 'Wolf Depredation Trends and the Use of Fladry Barriers to Protect Livestock in Western North America'

Yet prey vulnerability to wolf predation depends mostly on the presence and the identity of the other preys. Therefore, one must look at the relative vulnerability to explain prey selection, and not only the vulnerability of the sole prey species. If livestock vulnerability becomes lower than wild prey vulnerability, depredation is supposed to decrease and predation to increase, provided encounter rates and food intake are equivalent between livestock and wild preys [64].

However, we should not see relative vulnerability as something static. Wild prey and livestock vulnerabilities are constantly changing and dynamic. Increased vulnerability of wild preys due to harsh conditions in winter can for example deepen the gap between livestock and wild prey vulnerabilities, even several months after winter, which can have the effect of redirecting wolf attacks on wild preys (*e.g.* in Minnesota, [50]). Any state of increased vulnerability in livestock can also be exploited by wolves, as sick individuals or young [233]. For example, [234] showed that wolves in Italy selected domestic calves in early summer when they were just born, but that wolves reported their selection on sheep in late summer when calves had grown. Wolves of the same region turned on domestic abandoned goats mostly at the end of the grazing season only, probably because these goats were still protected before [222]. In France, it has been noticed that wolves were switching their attacks on livestock from night to day, when protection was loosened ([71], Fressard, in prep., H. Cotton, pers. com.).

[233]: Bangs et al. (2001), 'Managing Wolf Conflict with Livestock in the Northwestern United States'

[234]: Meriggi et al. (1996), 'The Feeding Habits of Wolves in Relation to Large Prey Availability in Northern Italy'

[71]: Meuret et al. (2021), 'Missing Shots: Has the Possibility of Shooting Wolves Been Lacking for 20 Years in France's Livestock Protection Measures?'

But before digging into the complexities of dynamic relative vulnerability, I will stick with two main scenarios of static relative vulnerability.

First scenario: wild prey are generally less vulnerable than most flocks of livestock. They could be so because of their larger size, body features (*e.g.* horns) or behaviour (*e.g.* high level of alertness, aggressiveness, adults surrounding young...), and because livestock has a low level of husbandry protection. In theory, wild preys would be mostly accessible to individuals or groups with high hunting efficiency, the other wolves (lone individuals, small groups of light or inexperienced individuals) being compelled to report their predation on more vulnerable preys as livestock.

Second scenario: wild prey are generally more vulnerable than most flocks of livestock. They could be so because they are small, defenceless or naive to predator (*e.g.* in newly wolf-recolonised areas), whereas livestock is highly protected. In theory, livestock would be mostly accessible to individuals or groups with high hunting efficiency, the other wolves being compelled to report their predation on wild preys.

Let's now consider the two other predation parameters, encounter rates and food intake, as equal between wild prey and livestock, and only vulnerability as unequal (scenario 1 or 2). If the optimal foraging theory is true, all wolves will try to maximise profitability. Then wolves should mostly point their predation on the most vulnerable prey, no matter their individual or pack hunting efficiency. In scenario 1, this means they will all tend to attack livestock, and in scenario 2 wild preys.

However, the optimal foraging theory could not apply as simply as presented. There could be individual or pack-related factors that could modify the wild prey and livestock vulnerabilities for certain wolves. These factors could increase or decrease both type of vulnerabilities at the same time, making both wild prey and livestock less or more vulnerable to a wolf's predation. These factors could also only modify the vulnerability of wild prey or livestock separately, meaning they change the relative prey vulnerability (the vulnerability ranking).

In short, in the same location and at the same time, some wolves could live under scenario 1 (livestock more accessible than wild prey), when others could live under scenario 2 (livestock less accessible than wild prey). I report two main factors affecting prey vulnerability: **hunting efficiency and learning**.

Hunting efficiency. As we have seen in section *Hunting groups* on page 61, hunting efficiency can be determined by the weight and age of wolves, and the size of their hunting groups. Increase in hunting efficiency allows wolves to decrease the general vulnerability of all types of prey, domestic or wild (but keeping relative prey vulnerability untouched). Therefore, hunting efficiency increases the accessible range of prey. We have seen for wild prey selection that several accessible preys (*i.e.* vulnerable prey) to wolves relax predation on one type of prey (*e.g.* [208] for elk and roe deer). Following this observation for wild prey selection, let's try to apply it to domestic-wild prey selection. In scenario 1, highly efficient hunters could therefore predate both wild prey and livestock, when less efficient hunters would mostly report their predation on livestock because of their reduced range of accessible prey. In scenario 2, livestock would only be accessible to the most efficient hunters.

The variations in individual or pack hunting efficiency is a nice assumption to explain varying individual or pack levels of depredation. What does the literature say about it?

In some cases, those which appear as the most efficient hunters seem to be less likely to depredate, therefore following assumption of scenario 1. In Italy, after the deaths of her breeding partner and her offspring, therefore reducing the largest possible hunting group size, a breeding female started to attack livestock [137], a result that was also observed for two other wolves in [50]. A starved-looking wolf has been repeatedly observed attacking the weakest or isolated sheep of a flock in France, despite the livestock guarding dog's presence (CERPAM, pers. com.). We can also relate the results of [51] who found that wolves in dispersion (*i.e.* alone) ate more livestock than wolves in pack, in what seems a scenario 1 (domestic goats were apparently poorly protected). However, territory knowledge could also explain this difference between pack and dispersers as we have seen previously. In Wisconsin, [230] found packs involved in depredations were neither small ($\leqslant 2$) nor large ($\geqslant 6$). A similar result was found in Queyras, France, where [201] found depredation risks increased for medium-sized packs (with the same thresholds of small or large packs). An assumption raised by [201] was that small pack had smaller food needs, therefore requiring less kills, when larger packs would have a larger accessible range of prey, therefore relaxing their predation on livestock. All of these results are related to pack size (a proxy for hunting group size). To my knowledge, there is no study which showed that younger wolves, lacking experience and not at their full size, are more likely to depredate than older wolves, supposedly better individual hunters. Only J.-M. Landry and J.-L. Borelli from IPRA felt they observed more subadults testing guarding dogs and attempting depredations than adults, because these individuals seemed more clumsy and inexperienced[2] [12].

2: as J.-M. Landry wrote in [12], p.306: '*Our preliminary results strongly suggest that subadults, neglected by the breeders until pups are grown enough to follow the group, are responsible for attacks on livestock.*'

[12]: Landry (2017), *Le Loup*

In other cases, those which appear as the less efficient hunters seem to be less likely to depredate, therefore following assumption of scenario 2. This was the case in Minnesota, where only removal of male adults (the most efficient hunters of large preys according to [214]) was effective to reduce depredation risks [97]. We should however not forget that it could be due to higher encounter rates too, as explained in section *Reproduction* on page 69. In Wisconsin, only healthy wolves were apparently causing depredations (but there were maybe no injured wolves). Several sources related that larger packs were more likely to depredate. In the American northern Rocky Mountains, risks of depredation recurrence was higher for larger packs [96]. It has been shown in Italy and in Wisconsin that packs also tended to attack more livestock than individuals in dispersion [137, 227] and than territorial lone wolves [227]. Yet these results could also be due to high encounter rates with livestock and high food needs in packs, especially in the big ones. It is therefore difficult to disentangle all these effects from each other. Nevertheless, the feelings of farmers in Greece [64] or in France [235] went in the direction that larger packs fared better with depredation as they could outnumber livestock guarding dogs and more easily outmanoeuvre their protection.

[235]: Candy et al. (2019), *Chiens de protection : Quand les éleveurs forgent leurs savoirs dans les Alpes*

Finally, in some studies there was no evidence that hunting efficiency modified depredation risks. Removing an adult was not more effective than removing a yearling to change depredation recurrences in Minnesota

[50]. Several studies or review showed no difference in depredation risk either between males and females [101, 227, 229], whereas males would benefit from a larger range of accessible prey thanks to their higher body size [214].

There could be several explanations for why hunting efficiency does not modify depredation risks in some cases. The differences in vulnerabilities should be notable between wild prey and livestock to expect that vulnerability has an impact on prey selection, but also to expect to statistically identify it. In addition, for hunting group size to have an effect on depredation, this implies that wolves actually hunt in groups. We have seen that hunting group size mainly depends on the size of the biggest and commonly available preys. If the available preys are small, as roe deer, and do not require a powerful group to kill it, then wolves may hunt alone in order to maximise food intake, and pack may consequently be relatively small (they do not have to share food with a large number of pack mates). This is typically the case in southern Europe, where wolves hunt roe deer or wild boar [51, 221] and notably the young of these species [223]. If wolves in these areas hunt wild preys alone, and if their behaviour during wild prey predation is similar to the one during depredation, then we should not expect prey vulnerabilities to be different between territorial lone wolves and those in packs (but encounter rates and food needs would not be equivalent between their territories, however).

Learning. As wolves could learn where to find specific preys across time (as we have seen in section *Hunting behaviour* on page 65), they could also learn how to successfully attack this type of prey and to exploit its vulnerability. The learning capacity of wolves has been mentioned in scientific literature [51, 71, 96], yet it remains quite unknown. So what do we know about the learning process?

Let's talk first about positive reinforcements, in other words, successful depredations favouring the recurrence of depredations. In Idaho and Montana, models showed that packs which are not known to depredate had only 5% of risks to depredate the next year, against 50% of risks for packs with known depredations the previous year [236]. This recurrence rate is also consistent with findings from [227, 230].

[236]: Hanley et al. (2018), 'Forecasting Cattle Depredation Risk by Recolonizing Gray Wolves'

Another way to assess positive reinforcements is to look at wolf diet through scat or stomach contents. If it is mostly dominated by livestock remains whereas wild preys are abundant in the environment, then one could assume a certain degree of specialisation of wolves to depredation, involving positive reinforcements. However, cautions must be raised because if wolves cannot easily access and consume killed livestock, this analysis does not properly represent the level of hunting success (let alone prey selection). The scientific literature mainly reported a selection of wild preys over livestock, meaning wolves do not heavily rely on livestock to feed. [229] showed that wild preys were selected by wolves over livestock, even when correcting for both livestock and wild prey abundances (and therefore for encounter rates), and even when both are abundant [224, 228, 234]. The low livestock vulnerability induced by a high level of protection could explain this preference [229]. In France, [221] confirmed this general tendency, the livestock consumption rates of

8 packs being 21-38% during summer; only one pack was being more dependent on livestock, with consumption rate of 50% the whole year. It has also been showed that wolves were not selective for wild prey or livestock in Italy [51].

These results are quite contradictory with observations on the ground, in which the mentions to assiduousness of wolves in depredation seem to involve more than a fifty-fifty risks of repeating depredations across time. Hence, [232] observed that wolves frequently returned to the same flocks, despite the presence of dogs. They even observed wolves that had learned when and where a flock protected by dogs was going to its resting area for the night [153]. This regularity around flocks was described by farmers in France as well[3], to hunt [235] or to consume killed livestock (H. Cotton pers. com., IPRA, 2018). This behaviour was sometimes described as '*clockwork*' (CERPAM, pers. com.). The switch from night to day in wolf attacks for some parts in France (Fressard, in prep., H. Cotton, pers. com.) also reported in Greece [64] suggests that some wolves have specifically adapted their behaviour to livestock vulnerability rate, at the expense of predation on wild prey. An illustrative example of predation specialisation on livestock would be the wolf called 'Billy' (*cfr.* Figure 2.7). Born in Germany, he dispersed through the Netherlands, Belgium, Germany again and arrived in France one year after its birth. Aside from the fact that he apparently attacked a large number of sheep during his travel, he was known to have developed the habit to kill domestic calves or cow including in sheds, in three countries and in a couple of months[4].

3: *'You know how it works when [wolves] succeed right? They stuck on you.'*, a farmer interviewed in [235], p.98



Figure 2.7: Wolf 'Billy' in front of a pen. Credits: J. Rottiers

4: To learn more about Billy's story: https://ofb.gouv.fr/actualites/loup-abattu-sur-la-commune-du-val-dajol

Apparent contradictions between the previous two paragraphs about learning and positive reinforcements could arise for several reasons (except the context-dependent ones). First, the time scale of recurrence is generally shorter for ground observations (*i.e.* over one or several weeks) than for these studies (from one year to the next). Second, the attacks could be the result of different packs, observers being unable to recognise with certitude wolves, where scientists might have access to genetic data. Third, studies mostly focused on pack-level rather than individual-level.

If wolves could learn to attack more livestock after repeated successes, it would make sense that they can also learn to avoid livestock after negative experiences. I will describe two levels of negative experiences usually employed to repel wolves from flocks.

The first and softer level of negative experience for a wolf is to exploit its phobia of novelty. For example, fladry (inoffensive plastic flags attached to a rope encircling flock) is designed for this purpose. Wolves have indeed been described as afraid of novel stimuli [81]. Several farmers in France reported that any unusual thing in the pasture (people, car...) seemed to repel wolves (CERPAM, pers. com.). However, this effect appeared effective only during a short period of time, a couple of days at the most, or several weeks or months for fladry [88]. In France, wolves sometimes attacked only a few hours after the departure of governmental agents from pastures, whereas these agents had seen the wolves roaming but keeping their distances with the guarded flock (H. Cotton, pers. com.). When I looked at the available operation reports of these governmental agents in France, and selected the 53 operations lasting four consecutive

[81]: Bangs et al. (2006), 'Non-Lethal and Lethal Tools to Manage Wolf-Livestock Conflict in the Northwestern United States'

[88]: Iliopoulos et al. (2019), 'Tools for Co-Existence: Fladry Corrals Efficiently Repel Wild Wolves (Canis Lupus) from Experimental Baiting Sites'

days (the usual operation duration) and involving no killed or injured wolves, I observed that 59% of them did not include any wolf observation (*cfr.* Figure 2.8). When they did, only 22% of operations observed wolves in several consecutive days. T. Escallier mentioned that the most striking behaviour he observed during his livestock protection operation was the wolf cautiousness, taking its time to approach flocks, sometimes turning around it at long distances. He saw on several occasions wolves fleeing when seeing and smelling him and his colleagues around the flock, or when surprised by their lights (louveterie lieutenants are required to light wolves before shooting). Only once a wolf showed no response to light: during the operation of a flock adjacent to village houses, as if the wolf was already accustomed to artificial light. All of this tends to confirm wolf neophobia. Nevertheless, J.-M. Landry and J.-L. Borelli who spent time to observe several packs in the French Alps [232] felt their new presence on open pastures did not disturb the wolves they observed whereas they were not hiding from wolves but these observers remained farther from the flock ($\sim 300 - 700m$) [237] than governmental agents ($\sim 200m$).

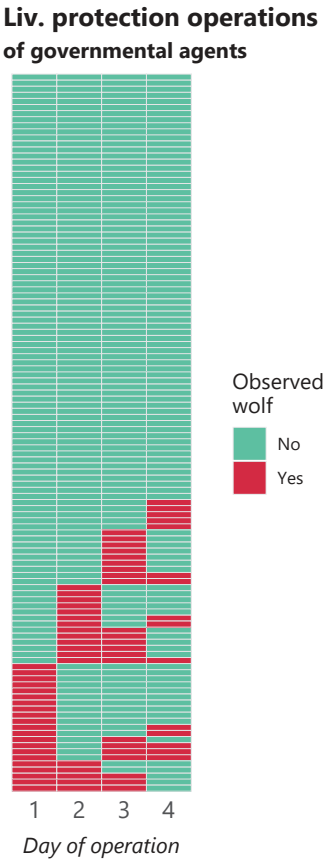

Figure 2.8: Sequences of wolf observations during 118 livestock protection operations lasting 4 nights, led by governmental agents in France. Each row represents an operation, each cell a day of operation. The ranking of the rows was only made for visual purposes. Credits: O. Grente

The second level of negative experience which can be employed is to prevent access to flock or to inflict temporary pain or excessive stress, such as fences (electrified or not), livestock guarding dogs or gun firing. Yet, if wolves confronted to the first level of negative experience learn that the new features are no threat, they can also learn to bypass the harmful features of the second level. In the French Alps, it has been observed that wolves kept returning to pastures guarded by dogs, and that successful attacks of wolves mainly happened when guarding dogs did not interact with wolves (isolated sheep, dogs not detecting wolves...) [232]. H. Cotton told me he once saw a wolf approaching his flock covered by bush, flattened as it was stalking some sheep on border of the flock, fleeing only when he yelled at it. This technique is the principal one used by wolves to attack his flock for several years now; this allows the wolves to stay unseen from the guarding dogs, but also from the flock which may alert the dogs by its movements [225]. This discretion using vegetation has been described by IPRA too in this video.

Wolves can bypass the challenge of non-electrified mobile fences by ploughing into them (S. Rigeade, pers. com.), and jump over the electrified ones. This video of IPRA is illustrative: a wolf is jumping over an electrified fence to attempt an attack, but jumps again to go out of the enclosure

[237]: Borelli et al. (2021), *Le loup dans le système pastoral. Rapport CanOvis IPRA-FJML 2013-2018.*



Figure 2.9: A wolf jumping an electrified fence at night to enter within a sheep pen, filmed by a camera-trap in the French Alps. The scene has been filmed with thermal camera too. The jumping wolf came out of the pen a few seconds later when a guarding dog reacted by barking and approaching. When it first entered the pen, another dog was sleeping very close to the jumping location and did not react to the wolf's jump. The other wolf (probably its breeding partner) which was also turning around the pen did not jump. The video can be accessed here. Credits: IPRA

when a livestock guarding dog is actively approaching and barking (*cfr.* Figure 2.9). Therefore, wolves can easily give up an attack if they feel there is a serious threat coming from dogs[5]. This brings to mind the predation behaviour of wolves that we previously described: wolves mostly attack running prey, and can give up if a big animal choose to face them [215]. However, wolves can sometimes persist even with defying prey [205], probably because they evaluate threat as manageable. This is something we can find in dog-wolf interactions. Wolves would not try to compete with active guarding dogs if they are outnumbered (IPRA, pers. com.) but are in some occasions able to attack guarding dogs, to injure them (CERPAM, pers. com.) or even to kill them at the pasture (H. Cotton, pers. com.).

5: or a threat coming from livestock itself, as this wolf running from cows in France after approaching them, see the video by IPRA here

Thus, some wolves are able to learn to exploit the vulnerabilities of flock protection systems. Humans have used two main possibilities to prevent this. First, we fill the gaps of the system the best we can, by improving the existent protections or by adding new ones. Second, we cull the wolves involved in livestock attacks. This second option rejoins the first assumption about the culling effects (Assumption 1). It suggests that, by culling those wolves, the depredation pressure is released on the pasture on a short term, and the artificial selection of the most fearful wolves in the population is engaged on the long term [71]. This implies that the capacity of wolves to exploit the vulnerabilities of prey protection systems (whereas it is domestic or wild) is not totally learned by experience and is facilitated by a genetically-defined boldness. If learning was indeed sufficient to overcome protection system, then any wolf testing long enough the system gaps would with certainty succeed to depredate one day or another. In this scenario, the artificial selection would not work, and the culling would only help farmer by temporarily releasing the depredation pressure (*i.e.* decreasing wolf numbers in the vicinity) before the arrival of other wolves.

To disentangle the responsibility of genetics and learning in the capacity to exploit vulnerabilities of flock protection system is difficult if not impossible in the wild (in short the difference between nature and nurture to explain depredation). Some observations can be interpreted in both ways. For example, it has been observed in the French Alps that two hunting adult wolves could behave differently in front of a fence, one jumping over to eat a carcass (another IPRA's video) or to attempt an attack (*cfr.* Figure 2.9). In Germany, it has been reported too (I. Reinhardt, pers. com.). Is it because the jumping wolf is naturally bolder than the other? Is it because this wolf learned that jumping was possible and sometimes rewarding? Is it both? It is hard to say, yet important to test assumption 2.

Until now, we only focused on individual learning. However, for a social species as *Canis lupus*, there could also be transmission of knowledge among pack members, especially vertical transmission between parents and offspring. The transmission can be positive reinforcement regarding depredation. This would suggest that a member from a pack with an individual likely to depredate has more chance to depredate than a wolf from a pack with no such individual. About this, you can read in [137], where a small study area has been intensively surveyed in the central Appennine ridge, Italy:

> *'In Pack 2, conversely, 80% of the members were involved in depredations, indicating a recurrent livestock hunting strategy. Interestingly, the hypothetical parental female of this pack [...] was the most active individual responsible for three attacks, in one of which she cooperated with an offspring, suggesting a cultural transmission of the predatory behavior.'* [137], p.108.

Transmission of knowledge between pack members could also be negative reinforcements regarding depredation. We generally expect the individual the most likely to depredate to influence the rest of its pack, yet wolves fearful of livestock protection could maybe also guide their hunting group to avoid livestock. This pattern might be reinforced if several members have bad experiences with livestock at the same time[6].

I looked at the 21 operation reports from governmental agents in France where they have seen at least two wolves together (*cfr.* Figure 2.10). One fourth of them (*Group 1*) has led to bad experiences for several wolves at the same time (*i.e.* two missed shots, four successful) without wolves being seen after on a short period of time (one or two additional nights). This might be an effect of negative reinforcements successfully spread at the group level. Yet we should not forget the potential fear of novelty previously described which could have applied for entire groups in one fourth of the operations (*Group 2*) even if no shot has been fired. On the contrary, missed shots were fired on groups of wolves (and a lone wolf) and showed no efficiency to prevent returns (*Group 3*), although the returning wolves were mostly seen alone and could have not been part of the group experiencing the missing shots. Finally, the agent's presence itself without shot did not seem to frighten wolves in the last fourth of operations (*Group 4*), where wolves kept returning to the guarded pastures. Therefore, the large diversity of cases and shortness of the operations made it quite difficult to conclude on the negative reinforcements simultaneously transmitted to pack members.

Interestingly, a recent study in the Netherlands specifically focused on the link between the depredation behaviour observed in individuals in dispersion and in their birth pack, in addition to proximity to humans [238]. Their sample size was very limited (14) and their determination of the behaviour of birth packs weakened by approximations. Yet their results showed a *'high degree of similarity in prey and habitat choice between parent packs and their loners'*. Individuals born in pack not known for depredation would have greater chance not to depredate themselves during dispersion, and vice-versa.

However, there is a parameter the study did not seem to take into account. As expected, dispersers were quite young (median age: 20 months), and 36% were less than a year. In Germany where the dispersers were born, sheep are kept in sheds from November to April[7]. This means that when they started to hunt with their birth pack from their first fall, sheep were probably already in sheds, and could still be in sheds when they dispersed. Hence, they could have been fed with sheep by their parents during their first months but would rather actively hunt on wild preys when in their birth packs. Therefore, I expect vertical transmission of depredation behaviour quite weak for young dispersers in countries where sheep are staying a long time in sheds as in Germany and in some parts of France. However, this does not exclude the eventuality that

6: In France, a farmer, whose flock was frequently attacked, shot simultaneously 2 wolves from a 5-wolf hunting group during a new attack on his flock. One died immediately, the other was found dead two days later. He said the attacks or attempts ceased and he even relaxed a bit the protection system. (CERPAM, pers. com.)

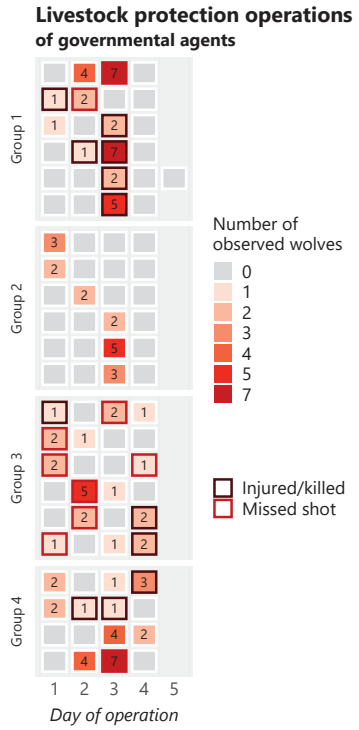

Figure 2.10: Sequences of wolf observations during 21 livestock protection operations with at least 2 wolves seen together, led by governmental agents in France. Each row represents an operation, each cell a day of operation. The first and last lines correspond to the same operation which is duplicated because it could go in both the analysis groups 1 and 2. Only operations lasting at least 4 days were selected. Only one wolf has been killed or injured in the corresponding cells. We assumed injury involved quick death. The ranking of the rows within groups was only made for visual purposes. Credits: O. Grente

[238]: van Liere et al. (2021), 'Conflicts with Wolves Can Originate from Their Parent Packs'

7: *pers. com.* of P. Verté from the Walloon public service (Belgium)

adults in the same pack would not learn from each other, and not being influenced by other pack member's hunting habits.

Food intake

After encounter rates and vulnerability, the last parameter which influences predation on wild prey is food intake. In this final part of the literature review, we will have a look at how this parameter can influence depredation.

It is quite easy to picture that a bigger pack on the same territory will have higher food needs that a lone territorial wolf or a small pack. In short, a higher density of wolves will increase food needs and predation pressure on the prey system (domestic or wild). We could believe there are compensatory responses to higher food needs that a pack could use:

- **Expand pack territory**. This would allow wolf density to locally decrease, therefore relaxing predation pressure. Yet it has been shown in Montana [151] and in Scandinavia [239], that big packs actually tend to have smaller territories. The reason would be a better position to defend the most profitable territory, which theoretically provides the highest of food resources (benefits) for the lowest size (costs, large territory being energetically costly to prospect and defend). A good territory could also help wolves to produce and raise more pups to adulthood, resulting in larger packs, which closes the loop.
- **Force individuals to leave the pack.** In short, to cause dispersion to also relax predation pressure. According to [151], this second possible compensatory response is preferred over the first one in wolves. If you want to learn more about dispersion in wolves, I let you go straight to Chapter 1 if you have skipped it.
- **Kill larger prey.** Large preys provide more food than small preys and are therefore more profitable. They are generally harder to kill, but this difficulty can be compensated by the increased higher hunting efficiency of large packs. The effect of this compensatory response has been discussed for wild prey predation in section *Size of hunting groups* on page 62 and for depredation in section *Hunting efficiency* on page 72.
- **Kill more prey.** This is the most straightforward compensatory response. This has the effect to increase predation pressure to provide all pack mates enough food intake. The results of studies showing that packs were more likely to depredate when large [96] or compared to lone wolves [137, 227] could be reflective of the higher rate of food needs, or of the higher hunting efficiency (that we have discussed about in section *Hunting efficiency* on page 72).

[151]: Sells et al. (2021), 'Evidence of Economical Territory Selection in a Cooperative Carnivore'

[239]: Mattisson et al. (2013), 'Home Range Size Variation in a Recovering Wolf Population: Evaluating the Effect of Environmental, Demographic,and Social Factors'

Yet there is a good way to differentiate the influence of food needs and those of hunting efficiency linked to changes in pack size. The key is to separate adults and pups in the analysis. Pups are indeed more mouths to feed from when they are born in late spring but they do not contribute to hunt until their first fall (section *Season effect on hunting groups* on page 64). We have seen that generally dispersers leave their pack before pup birth or do so after pup's integration to hunt (Chapter 1). Consequently, from

pup's births to fall, food needs are increasing, but pack hunting efficiency is not, whether wolves hunt alone or not.

In several studies, the peak in numbers of wolf depredations corresponded to the period of pup's growth. In Minnesota [50], a first peak occurred in May but certainly corresponded to the accessibility of newborn domestic calves. The second peak occurred in August-September whereas livestock was already pasturing for a couple of months. Depredations then decreased from fall. The same late-summer peak is observed in France too, in pastures at high altitude, whereas livestock is generally present for several months already. In southern Europe, depredation peaks seemed delayed and happened in early fall in Greece (*cfr.* Figure 2.11, [64]) and in Italy [240].

[240]: Ciucci et al. (1998), 'Wolf and Dog Depredation on Livestock in Central Italy'

Livestock's presence and abundance on pastures explained a big part of these depredation annual variations (depredations being mostly absent in winter when livestock is in sheds). However, they did not explain why peaks did not occur at the arrival of livestock on pastures in late spring but later (except for the May peak in the USA). This could be evidence that the increased food needs led to an increase in the number of depredations. In addition, wolves and especially breeders are more spatially constrained during the raise of their pups (*cfr.* Figure 2.6).The proximity of pastures to *rendez-vous* sites or tracks leading to it could increase encounter rates and therefore depredation risks, as observed by [50]. S. Rigeade also observed that the most attacked farmers around his pastures were close to where he estimated *rendez-vous* site locations with his camera-traps.

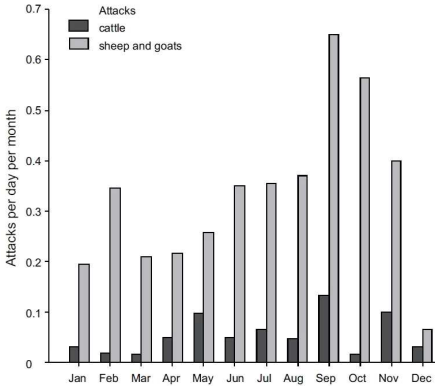

Figure 2.11: Monthly rate of wolf depredations on domestic cattle (black) and sheep or goats (grey) in central Greece, in 1999 and 2000. From Iliopoulos *et al.*, 2009.

However, these depredation peaks in late summer could also result from the decrease in the vulnerabilities of young of wild prey, as they grow too and become less accessible [50, 240]. Therefore, wolves could report their successful attacks on livestock, resulting in depredation peaks, and being unrelated to increase pack food needs. This could explain why [230] did not find a significant correlation between the number of pups in pack and the number of depredations in Wisconsin.

Food needs can also be expressed at the individual level, and not only the pack level. Hungry wolves could be pushed to take more risks to eat, including defying livestock protection systems. For example, the same wolf could show boldness or fear in front of the same livestock protection system in a short period of time, maybe related to its level of hunger [232].

The wolf depredation behaviour recap

The depredation behaviour in wolves depends on three parameters related to domestic and wild preys: **encounter rates between wolves and preys, relative vulnerability of preys and food needs of wolves within a single territory**. Encounter rates might be modified by the resident status, the reproductive status or the stay duration on a territory. Relative prey vulnerabilities might be modified by the hunting efficiency and learning abilities of wolves. Food needs of wolves are mainly modified by the number of wolves within a territory.

Through our literature review, we have seen a lot of contradictory

results. This comes from two main reasons. First, there are multiple wolf depredation contexts within the wolf's range. The identity and abundance of preys vary a lot from one place to another, therefore modifying pack size and food needs among others. Thus, what can be seen in an area can be totally different in another. In addition, it can be hard to disentangle the influences of each parameter (encounter rates, prey vulnerabilities and food needs) from one another within studies, leading to uncertain conclusions.

2.3 Modelling

In this section, I will describe how we completed the IBM from Chapter 1 by incorporating the two remaining components about the wolf depredation behaviour and the depredation management by culling. We saw in section *Aim of the chapter* on page 57 of this chapter that we developed this IBM to test different scenarios in which some wolves are more likely to depredate than others based on their individual or pack characteristics only, and to observe the effects of basic culling policies in response to these configurations. The model is not spatially-explicit here, and the modelled wolves are supposed to evolve in the same environmental context: the sheep and wild preys are uniformly distributed within the virtual environment (*i.e.* all wolves with the same individual and pack characteristics have the same access to the same domestic or wild preys).

The depredation behaviour component

The tested hypotheses

The literature review showed that the wolf depredation behaviour is multifactorial, even when considering a single environment. The effects of individual or pack characteristics on depredation are still mostly debated and can depend on the environmental context. Each possible effect has to be tested under the form of an *hypothesis*, as in Chapter 1.

However, the more hypotheses you add, the more combinations or *scenarios* you get. It rapidly becomes very tedious to explore every scenario, whether you talk about computational time or result interpretation. This is why we had to make a choice concerning the wolf characteristics and their associated hypotheses to test in the IBM when defining the wolf depredation behaviour component.

- **The hypotheses about wolf characteristics that we did not incorporate in the IBM.**
    1. ***Resident status***. Territorial wolves and wolves in dispersion do not have the same encounter rates with prey.
    2. ***Reproduction***.
        - Individual level: The breeding wolves have higher needs to kill prey to feed their pups than the other wolves of their pack, which can increase the breeder's rate of depredations.

- Pack level: A reproductive pack will also be more spatially constrained around the den and *rendez-vous* sites, which can increase or decrease its encounter rates with livestock.

3. ***Territory knowledge***.
   - Individual level: Wolves living on a long period in the same territory have a better knowledge of livestock localisations, and a higher encounter rate with them.
   - Pack level: Wolves of the same pack are influenced by the territory knowledge of the other pack members concerning livestock localisations.
4. ***Hunting efficiency***. Female wolves are less efficient than male wolves to hunt large or preys of low vulnerability.
5. ***Learning***. The ability of wolves to bypass livestock protection system is not only learned by experience but also facilitated by a genetically-defined personality traits.
6. ***Food intake***. Some wolves, because of a temporary hunger or bad conditions, will attempt more attacks even on risky preys.

We did no test the hypothesis 1 and the hypothesis 2 at the pack level mainly because the IBM was not spatially explicit and we conditioned an uniform distribution of prey. Moreover, hypothesis 1 was partly incorporated under the tested hypothesis (i) that we will see right after.

The hypothesis 2 was not incorporated because we thought that the presence of pups generally impacted all the members of a pack and not only the breeders. Because breeders are busy to feed their pups, they could have less food to share with the other pack members that could in turn need to hunt more too compensate. The pup's presence in a pack then may increase the hunt searches for all pack members, and so the encounter rates with livestock.

We did not incorporated hypothesis 4 because our model is focused on southern Europe where preys are not as large as in the studies where this result has been found.

Finally, we put aside the hypotheses 3, 5 and 6 because they lacked support from literature review or observations in the field (*i.e.* there was no strong evidence found in articles or directly from the field).

This let us with four main hypotheses to test in the IBM.

- **The hypotheses about wolf characteristics that we incorporated in the IBM.**

  (i) ***Territory knowledge***.
  - Individual level: Wolves living on a long period in the same territory have a higher encounter rate with wild preys, which decreases their depredation risk.
  - Pack level: Wolves of the same pack are influenced by the territory knowledge of the other pack members concerning wild prey localisations.

  (ii) ***Hunting efficiency***.
  - Individual level: Adult wolves are more efficient than subadults to hunt.

- Pack level: Larger hunting groups are more efficient than smaller hunting groups to hunt low-vulnerable preys, especially if these groups are composed by adults.

(iii) ***Learning***.
- Individual level: Some wolves learn to bypass the livestock protection system (positive reinforcement), which increases their depredation risk, when others learn to avoid it (negative reinforcement), which decreases their depredation risk.
- Pack level: Breeders can transmit their learnings to each other and to subadults when hunting in groups. Subordinates can influence each other when hunting in groups.

(iv) ***Food intake***. A higher number of wolves within the same territory results in higher food needs, which increases the risk of depredation in the territory.

We chose to test the hypothesis (i) related to wild preys only, and to reject the previous hypothesis 3. This choice was explained by two reasons. First, we wanted to separately test the hypothesis that wolves knowing less their environment (because they are newly established or still in dispersion) would be less efficient to encounter wild preys. This hypothesis is indeed generally prevalent in the more general assumption of culling reinforcing depredations (Assumption 2). Second, by incorporating the hypothesis (iii), we supposed a positive reinforcement of depredation as possible, which could be seen as a better ability to bypass livestock protection but also to find flocks (therefore rejoining hypothesis 3).

The other hypotheses that we chose to test, (ii), (iii), (iv), were partly supported in the scientific literature or by field observations. Both hypotheses (ii) and (iii) were required to test the two general assumptions on culling effects (Assumption 1 and Assumption 2).

The hypotheses were then tested under the scenario scheme (*cfr.* Figure 2.12), as in Chapter 1. For each hypothesis, the scenario could test the hypothesis at the individual level and/or the pack level. For each level of an hypothesis, the hypothesis as stated above could be tested in the scenario (*i.e.* H_1), or could not be tested (*i.e.* the scenario would test the null hypothesis H_0). We conditioned that the selection of H_0 at the individual level would compel the pack level of the same hypothesis to be selected as H_0 too (but the pack level does not compel the individual level). Indeed, we found hardly justifiable that a biological process assumed not to apply at the individual level could apply at the pack level.

There were three exceptions to this scenario scheme. First, the hypothesis (iv) about food needs was only tested at the pack level. Second, this hypothesis was in fact not tested as an hypothesis strictly speaking because there was no null hypothesis associated to it. This meant that in every scenario, the hypothesis (iv) was assumed as true: a higher number of wolves within the same pack resulted in higher food needs. We felt this statement was sufficiently supported in literature to be modelled without testing a null hypothesis. This did not mean that larger pack will systematically depredate more in our model, as the other hypotheses could still influence depredation (especially hypothesis (ii) concerning pack size). It only implied that larger packs will require by killing larger preys and/or more preys.

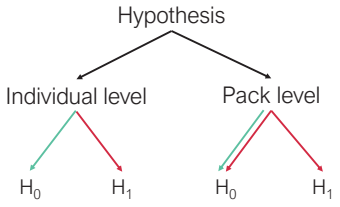

Figure 2.12: The decision tree used in the IBM for each tested hypothesis of the depredation component. The colours represented the possible combinations of hypothesis version (H_0 or H_1) at the individual and pack levels that could be found in a scenario. To select H_1 at the pack level, H_1 must be selected at the individual level. A scenario was ultimately a compilation of all the decisions made for each tested hypothesis. Credits: O. Grente

The third exception to the scenario scheme was about the hypothesis (ii). It was the only hypothesis divided into two mutually exclusive sub-hypotheses H_1 and H_2 which were presented during the literature review: H_1 considered livestock as more vulnerable than wild preys, and H_2 considered livestock as less vulnerable than wild preys. Because they were mutually exclusive, H_1 and H_2 could no coexist at the individual and pack level (but it was still possible to have a null hypothesis for only the pack level and not the individual level).

This being said, an example of scenario tested in this chapter could be: H_0 for hypothesis (i) at both individual and pack levels, H_2 for hypothesis (ii) at both individual and pack levels, H_1 for hypothesis (iii) at individual scale, H_0 for hypothesis (iii) at pack scale and necessarily H_1 for hypothesis (iv).

The depredation index

This is the section where we translated what was observed or assumed in the wild into computational rules. In short, modelling.

As we have said, the IBM was not spatial. Therefore, there was no possibility to model spatial interactions between wolves and sheep[8]. The attacks or attempts of attacks could not therefore be directly modelled. Even if we had decided to model a spatial IBM in the first place, the model would have been much more complex, as we would have required to model all the movements of wolves, livestock and wild preys.

8: If you want to test a simple spatially explicit IBM with wolves and sheep, you can play with this interactive web-based model from NetLogo.

Instead the idea was to attribute to each wolf a **Depredation Index (DI)**. For simplicity, we did not attribute a DI to pups as they generally start to hunt when subadults.

Definition 3 *The Depredation Index (DI) is a characteristic attributed to each wolf of the IBM. The DI describes the inclination of a wolf towards depredation. Its range is* $[-1, 1]$*. The DI value is interpreted as:*

- *DI close to* 1*: the wolf is highly inclined to depredations, to the detriment of predation on wild preys.*
- *DI close to* 0*: the wolf is as inclined to depredation as to predation on wild preys.*
- *DI close to* -1*: the wolf is poorly inclined to depredations and favours predation on wild preys.*

DI was calculated for each wolf after the *Reproduction* and *Aging* submodels of the IBM, but before the *Mortality* submodel. The effects of a wolf's characteristics on its DI depended on the scenario, in other words on the hypotheses that made up the scenario (see section *The tested hypotheses*). To calculate the DI, four steps were used. The details of steps 1-3 for each hypothesis is described in Table 2.1.

- **The calculation steps of the DI of a wolf.**

  1. **Extract the individual characteristics.** For each tested hypothesis, a wolf's characteristic in relation to the hypothesis was extracted under a numeric format. If a scenario involved a null hypothesis H_0 at the individual level, the extraction

of the wolf's characteristic was not done. In addition, the hypothesis (iv) about food needs was never concerned by this extraction, as it was not studied at the individual level as said previously. For the three other hypotheses (i), (ii), (iii), the extracted individual characteristic value was abbreviated as following:

- Territory knowledge: ITK
- Hunting efficiency: IHE
- Learning: IL

2. **Extract the pack characteristics.** For each tested hypothesis, a wolf pack's characteristic in relation to the hypothesis was extracted under a numeric format. If a scenario involved a null hypothesis H_0 at the pack level, the extraction of the pack's characteristic was not done. In addition, for some specific wolves (*e.g.* alone, or in dispersion, see Table 2.1), this value was not extracted either.
   The extracted pack characteristic value was abbreviated as following according to the corresponding hypothesis:
   - Territory knowledge: PTK
   - Hunting efficiency: PHE
   - Learning: PL
   - Food intake: PFI
3. **Rescale the characteristic values.** The DI calculations (see next point) require a rescale of some of the extracted characteristic values (individual or pack) for two reasons:
   - The DI ranged on $[-1, 1]$, whereas some characteristic values did not. The concerned characteristic values should be scaled down to conform to the DI range and have a range equal or lower than the DI range $[-1, 1]$. We used the rescaling formula given in Equation 2.1.
   - The highest possible characteristic value should match with the highest risk for depredation (and vice-versa). For example, the highest value of ITK (stay duration) originally corresponded to the lowest risk of depredation; it was therefore necessary to rescale the values of ITK, by switching the minimum and maximum of its range. It was a specific case of rescaling that we called 'reverse scaling', and just required to reverse the number signs from positive to negative of the results of Equation 2.1.

$$v_r = \frac{new_{max} - new_{min}}{old_{max} - old_{min}} \times (v - old_{max}) + new_{max} \quad (2.1)$$

where v was the value to rescale, v_r was the value once rescaled, old_{min} and old_{max} were the original minimum and maximum values that could take v and new_{min} and new_{max} the new (*i.e.* rescaled) minimum and maximum values that could take v_r.
Example : The original range of v is $[0, 5]$ and its rescaled range is $[0, 1]$. For values of v equal to 0, 1, 2, 3, 4 and 5, the rescaled values v_r are 0, 0.2, 0.4, 0.6, 0.8 and 1.

4. **Calculate the DI.**
   a) The first step was to average the rescaled individual and pack characteristic values for each hypothesis (Equation 2.2).
      In some cases, the pack characteristic value was not extracted (for specific individuals or because of a null hypothesis). In these cases, the rescaled individual characteristic was used as such, without average. For hypothesis (iv), only a pack characteristic value (PFI) was extracted, and the rescaled PFI was also used as such, without average (Equation 2.2).
      If a scenario involved H_0 at both the individual and pack level for the same hypothesis, then the concerned hypothesis is considered as *inactive* and will be discarded

$$TK = \frac{ITK + PTK}{n_{TK}}; HE = \frac{IHE + PHE}{n_{HE}}$$
$$L = \frac{IL + PL}{n_L}; FI = PFI \quad (2.2)$$

where n_{TK}, n_{HE} and n_L were equal to 2 if the respective characteristic values were extracted at both individual and pack levels (*i.e* the hypothesis was averaged at both the individual and pack level), or equal to 1 if it was true for only one level.

from the final DI calculation.

b) **The DI was calculated as the mean of the rescaled characteristic values of all the active hypotheses, which were individually-pack-averaged or not depending on the situation.**

$$DI = \frac{TK + HE + L + FI}{N} \tag{2.3}$$

where N was the number of active hypotheses. Because FI was always active, the range of N was therefore $[1, 4]$. An inactive hypothesis should be considered as equal to 0 in this equation (*i.e.* discarded).

Specific case. The extraction of individual or pack characteristic values required to specify specific cases for some individuals, depending on the hypothesis.

- **Territory knowledge hypothesis:** It appeared quite reasonable to model that an individual in dispersion did not know its environment and had an ITK of 0. We also assumed that newly-established individuals (individuals which had just established on a territory the previous cycle) were naive regarding their new environment that they were discovering just as a disperser. We attributed an ITK of 1 to subadults which stayed in their pack (*i.e* who were not adopted; dispersal did not happen yet as DI is calculated before this submodel), because we considered pups to have an ITK of 0 (naive regarding their territory).
  PTK did not apply to dispersers or loners (alone territorial individuals) which had no pack's mates.

- **Hunting efficiency hypothesis:** We set PHE to 0 for loners and dispersers to deepen their reduced total HE compared to packs. For example, an adult from a pack with only another adult had a total HE of $((IHE = 1) + (PHE = 2))/2 = 1.5$ while a loner would have had a total HE of 1/1=1 if its PHE was not extracted, whereas with PHE set to 0, its HE was now (1+0)/2 = 0.5.

- **Learning hypothesis:** Because pups do not participate to hunting for most of their first year, especially livestock hunting (as they integrate the hunting groups when most of livestock is generally back in sheds), we considered that subadults (wolves of 1 year) were naive regarding individual learning of depredation. If we had wanted to model genetic differences between individuals (relative to the hypothesis 5 not incorporated), we could have set the subadult's IL with varying values.
  We considered that a breeder was only influenced by the hunting learnings of the other breeding wolf if any, as they could pair for hunting and subordinates did not seem to lead breeder's hunt [153]. Subordinates have been seen hunting with the breeding pair but also with the other subordinates only [153], explaining why we modelled that the subordinate's PL was influenced by the IL of all the other pack member's.
  PL did not apply to disperser or loner which had no pack's mates.

- **Food intake hypothesis:** PFI was equal to 1 for lone individuals (dispersers and loners), as '1 mouth to feed' in comparison to wolves in pack, where PFI would be at least equal to 2. PFI was extracted at the pack level for convenience with the other hypothesis, but would rather be seen as an Area Food Intake regardless of the presence of a pack.

Range capping. The capping of the highest value of some characteristic value range during extraction (steps 1-2) was sometimes necessary. The extension of the lowest value of PFI was also necessary during rescaling (step 3). Let me explain point by point.

- **Territory knowledge hypothesis:** The maximum stay duration of a wolf on a territory in our IBM could reach its entire life, limited at 15 years. However, we expected that the knowledge of a territory could not increase indefinitely. Yet there was no available information in the literature to rely on. In addition, the territory knowledge curve may be very context-dependent (being certainly more progressive in more complex ecosystems). Here, we chose to cap the maximum territory knowledge after 5 full years on the same territory (*i.e.*. from the 6th year on the same territory). This choice was therefore arbitrary and its effects should be tested with a sensitivity analysis.

- **Hunting efficiency hypothesis:** As we have seen in section *Size of hunting groups* on page 62, the group hunting efficiency tended to cap with group size, meaning that adding wolves did not improve the hunting success of a group of wolves and could even slightly decrease it. This optimal hunting group size depended on the size of the available preys. Our IBM focused on European wolf populations. We decided to cap PHE to 4 (*i.e.* 4 adults in a pack) as the hunting efficiency of one of the largest available preys in Europe, the red deer, peaked at 4 wolves [210]. For simplicity, we considered here that group hunting, if any, would generally include the whole pack as packs are small in our model.

- **Food intake hypothesis:** The capping of PFI was only for methodological reasons. The maximum pack size in our IBM was determined by a normal distribution. This meant the maximum pack size encountered during a model simulation was not fixed, and varies among simulations. In most simulations, it was around 6 (*mean maximum pack size* + *sd*) but for some simulations, it could have been 8 for example. To be able to compare PFI of wolf packs among simulations, it was therefore necessary to cap PFI, and we chose the cap of 6 to correspond to the generally encountered maximum pack size.
  The rescaling of PFI (step 3) had also the particularity to be extended to 0 (the rescaled minimum value). This meant that in Equation 2.1, old_{min} was intentionally set to 0 whereas it should have been 1. This way, for dispersers and loners (PFI equal to 1), their rescaled PFI was not equal to 0 but to 0.17. Having a PFI of 0 would not have make sense as it would have corresponded to a complete absence of food need in a wolf area, which was not true even for lone individuals.

Table 2.1: Details of the extraction of the individual (step 1) and pack (step 2) characteristic values applied for each wolf (except pups), and the rescaling of the characteristic values (step 3), according to the hypothesis. If the wolf fell in a specific case mentioned in the 4th column, its characteristic value extraction or recalling did not follow the general path (3rd column) but a specific path (4th column). The † symbol indicated that the highest value of a range was capped or that the lowest value of a range was extended. More explanations were provided in the paragraphs *Specific case* and *Range capping* in the main text.

Hypothesis	Step	Characteristic value	Specific case	Range
Territory Knowledge (i)	1	ITK = stay duration of the wolf on its territory in years	$ITK = 0$ for dispersers and newly-established individuals. $ITK = 1$ for subadults except adopted ones with $ITK = 0$	$[0, 5^{\dagger}]$
	2	PTK = the highest ITK of the pack.	PTK was not extracted for dispersers or loners	$[0, 5^{\dagger}]$
	3	Reverse scaling of ITK and PTK on $[-1, 0]$		$[-1, 0]$
Hunting Efficiency (ii)	1	$IHE = 1$ for adults and 0.5 for subadults		$\{0, 0.5, 1\}$
	2	PHE = sum of the IHE of all members of the pack	$PHE = 0$ for dispersers and loners	$[0, 4^{\dagger}]$
	3	H_1 (livestock more vulnerable than wild preys): ► $IHE = -1$ for adults and 0 for subadults ► Reverse scaling of PHE on $[-1, 0]$		$IHE \in \{-1, 0\}$ $PHE \in [-1, 0]$
		H_2 (livestock less vulnerable than wild preys): ► $IHE = 1$ for adults and 0 for subadults ► Rscaling of PHE on $[1, 0]$		$IHE \in \{0, 1\}$ $PHE \in [0, 1]$
Learning (iii)	1	$IL = DI$ of the previous cycle	$IL = 0$ for subadults	$[-1, 1]$
	2	For breeder: $PL = IL$ of the other breeder if any. For subordinates: PL = mean of the IL of all the other pack members	PL is not extracted for lone breeders, loners and dispersers	$[-1, 1]$
	3	∅		
Food Intake (iv)	1	∅		
	2	$PFI = N_{wolf2+} + (1/2 \times N_{wolf1})$ where N_{wolf2+} is the number of wolves of 2+ years old and N_{wolf1} is the number of pups of the pack	$PFI = 1$ for dispersers and loners	$[1, 6^{\dagger}]$
	3	Rescaling of PHE on $[0, 1]$		$[0^{\dagger}, 1]$

Before moving to the next section, let's see a simple example where we calculated the Depredation Index DI of 4 wolves on two time steps. Because a wolf's DI calculation was depending on the scenario and its involved hypotheses, we chose an illustrative scenario described in Table 2.2. Do not forget that we always considered the fourth hypothesis about food intake (iv) as stated, which explains why it does not appear in the table (*i.e.* H_1 always ticked for PFI). We can now move on to the extraction of the individual and pack characteristic values (steps 1-2), their rescaling if any (step 3) and the final DI calculation (step 4). Results are provided in Table 2.3.

Table 2.2: Example of DI scenario.

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE			✓
PHE			✓
IL		✓	
PL	✓		

Table 2.3: DI calculations for 4 individuals on two time steps following the illustrative scenario from Table 2.2. The symbol × means that the characteristic value was not extracted for this individual and hypothesis. The symbol ∅ means the individual was not territorial. The cells of ITK, PTK and PL columns are darkened because they did not contribute to the DI calculation (because their H_0 was selected in this scenario) and are displayed here for information only. The DI is calculated after the mortality event, here with the formula $(HE + L + FI)/N$ adapted from Equation 2.3. The table displays the information obtained at the end of two illustrative time steps.

					Steps 1-2							Step 3							Step 4
	Individual	Ind. ID	Pack ID	Age	ITK	PTK	IHE	PHE	IL	PL	PFI	ITK	PTK	IHE	PHE	IL	PL	PFI	DI
Time 1	Disperser	1	∅	2	0	×	1	0	0	×	1	0	×	1	0	0	×	0.17	0.22
	Breeder	2	1	4	3	3	1	2	0	0	2.5	-0.6	-0.6	1	0.5	0	0	0.42	0.39
	Breeder	3	1	3	1	3	1	2	0	0	2.5	-0.2	-0.6	1	0.5	0	0	0.42	0.39
	Pup	4	1	1	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Time 2	Loner	1	2	3	0	×	1	0	0.22	×	1	0	×	1	0	0.22	×	0.17	0.30
	Breeder	3	1	4	2	2	1	1.5	0.39	×	2	-0.4	-0.4	1	0.375	0.39	×	0.33	0.47
	Subordinate	4	1	2	1	2	0.5	1.5	0	0.39	2	-0.2	-0.4	0	0.375	0	0.39	0.33	0.17

In this example, the individual with ID 3, a breeder, had the highest risk of depredation (Table 2.3) in Time 2. This is explained because in the used scenario (Table 2.2), the IHE and PHE sub-hypotheses H_2 were active. Therefore, the most efficient hunters (here adults with pack's mates as individual 3) will have an easier access to livestock whereas the others will not. Because we set the IL at 0 for all the wolves in Time 1 (see why in the next section *Modelled population* on the following page), it had a minor influence in Time 2.

If we replace the IHE and PHE sub-hypotheses H_2 by H_1 in the scenario of Table 2.2, what are the changes on the wolves' depredation indices? The breeder with ID 3 became the individual with the lowest DI (-0.16) in Time 2, but the loner was not far, with a DI of -0.15 (Table 2.4). This is due to the fact that PFI remained high for this breeder compared to the loner, despite the effect of IHE and PHE which decreased the breeder's DI. The subordinate was the most likely to depredate with a DI of 0.05 in Time 2, mainly because its IHE did not decrease its DI.

Table 2.4: Simplified example equivalent to Table 2.3 but with H_1 for IHE and PHE. Only informative columns for the calculation of DI are displayed. I.ID and P.ID mean Individual ID and Pack ID respectively.

					Step 3				Step 4
	Ind.	I.ID	P.ID	Age	IHE	PHE	IL	PFI	DI
Time 1	Disp.	1	∅	2	-1	0	0	0.17	-0.11
	Breed.	2	1	4	-1	-0.5	0	0.42	-0.11
	Breed.	3	1	3	-1	-0.5	0	0.42	-0.11
	Pup	4	1	1	×	×	×	×	×
Time 2	Loner	1	2	3	-1	0	0.22	0.17	-0.15
	Breed.	3	1	4	-1	-0.375	0.39	0.33	-0.16
	Sub.	4	1	2	0	-0.375	0	0.33	-0.05

Let's summarise the depredation component of the IBM

We focused on 4 hypotheses to model the risk of depredation for each wolf according to its intrinsic characteristics. The first hypothesis is linked to encounter rates and assumes that wolves settled for a long period know well how to encounter wild preys within their territory, which has the consequence to relax depredation. The second hypothesis is linked to relative prey vulnerability and assumes that wolves with high hunting efficiency have a large range of optimal preys, which induces an increase of depredation risk for these wolves in the case where livestock is less vulnerable than wild preys. In the opposite case, it assumes wolves with low hunting efficiency target

livestock because wild preys are less accessible to them. The third hypothesis is linked to relative prey vulnerability too, and refers to the ability of wolves to learn to bypass livestock protection or to avoid it, which increases or decreases their depredation risks respectively. The fourth hypothesis is linked to food intake and assumes that a higher density of wolves in the same territory involves higher food needs, therefore increasing depredation risks even at the individual scale.

Modelled population

As mentioned before, we modelled our population within a unique environmental and pastoral context, in order to answer to the question raised in section *Aim of the chapter* on page 57: *'why, in the same environmental-pastoral context, some wolves depredate when others don't? Is it linked to the characteristics of the wolf or of its pack?'*

We opted to model an area equivalent to the study area of [190]: *'4000 km^2 of the Ligurian, Maritime, and Cozie ranges of the Western Alps in Italy and France'* (*cfr.* Figure 2.13). It had two advantages. First, this wolf population and its structure were thoroughly monitored, giving us interesting insights. Second, this wolf population was directly connected to the one found in the French Alps, in the same mountainous area where we found most of depredations of wolves in France. We could therefore expect similarities between the wolf population in [190] and our wolf population of interest in France.

[190]: Marucco et al. (2009), 'Wolf Survival and Population Trend Using Non-Invasive Capture-Recapture Techniques in the Western Alps'

In [190], they counted up to 7 packs the same year. For convenience and because we had not the objective of strictly representing their population, we decided to model up the carrying capacity of our IBM to 10 territories (filled by packs or loners). Over their 7 years of monitoring, [190] identified 87 individuals, including 18 dispersers, which for 6 of them moved outside the study area (*i.e.* emigrants). No information was given about the potential immigrants.

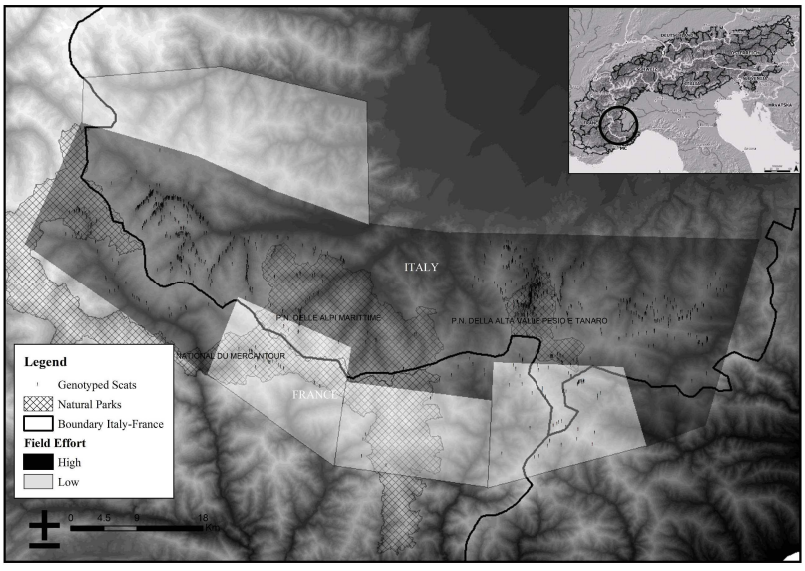

Figure 2.13: The study area in Marucco et al., 2009 [190]: *'4000 km^2 of the Ligurian, Maritime, and Cozie ranges of the Western Alps in Italy and France'*. We derived parameters from the monitoring of this wolf population for our own modelled wolf population.

In accordance with these results, we modelled that 6/18 = 33% of the dispersers found in our modelled population would emigrate each year. We could have modelled this rate a bit lower, given the fact that among the dispersers found in [190], some could have been immigrants from other areas. We did not change the immigration modelled in Chapter 1 with a number of immigrants per time step drawn within the fixed set of $\{0, 1, 2\}$. We did not change the other IBM parameters either (*e.g.* the mortality parameters).

Once we had decided the population parameters, we had to initialise the model with individuals. In Chapter 1, the initial population was comprised of 43 individuals and 10 packs, with a carrying capacity of 30 packs. The population in this chapter however was much smaller, and its initialisation was therefore riskier. Indeed, the IBM results of small populations can be consequentially influenced by the individual composition of the initial population, especially if the model is computed on a small number of time steps. The idea was then to constrain as little as possible our model by the initial population.

We therefore opted for a solution which could appear quite radical: to provide no initial population. Thanks to the immigration submodel, some immigrants colonise the area. It would take a while before having the whole modelled area colonised, but this option had big advantages. The population built up itself, without being constrained by an arbitrary initial choice. Thus, we introduced more variability in our model since the first time step, and we increased the range of possibilities in terms of population composition. Moreover, the DI also built up itself.

There was actually only one condition that we included in the first time step of the model: the number of immigrants was not drawn among $\{0, 1, 2\}$, but was compulsorily equal to 2, in order to speed up the colonisation (and to reduce computation times). Except this condition, the *Immigration* submodel was applied as it is in Chapter 1. The first time step therefore started at the *Immigration* submodel (as there was no initial population). Then, the other submodels were triggered in the same order of *M*1 in Chapter 1. However, because there could be no migrating pups in this first time step, adoption was not possible, and the only establishment possible at this time were in pairs (if the two initial immigrants were a male and a female) or alone. From the 2nd time step, the model followed *M*1 as in Chapter 1. Even if it was not be used until the culling submodel was triggered (see section *The culling scenarios* on page 95), the DI was calculated at all time steps from the first just, before the *Mortality* submodel (*cfr.* Figure 2.14).

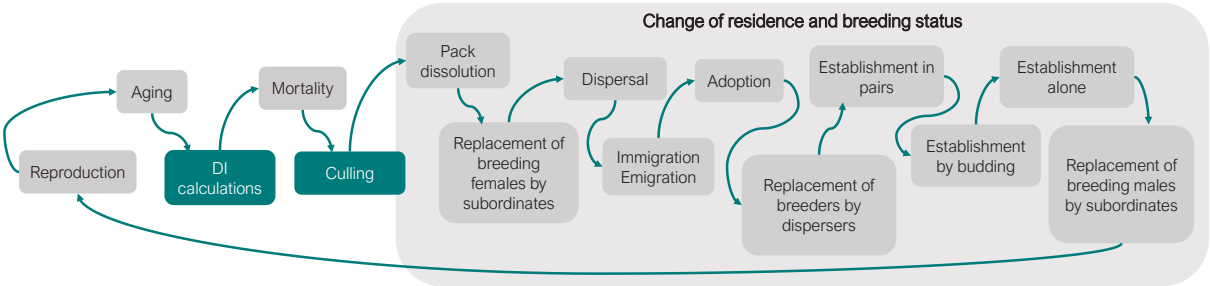

Figure 2.14: The IBM cycle from Chapter 1 with the added depredation and culling components. Credits: O. Grente

At one point, the impulse of immigrants within the modelled area allowed the full colonisation of the area by reproductive packs. We considered the time for colonisation was reached when the population size of a large majority of the simulations stabilised without culling applied.

The culling component

Now that we attributed to each wolf a depredation index, it is time to model the management of attacks by culling. The main goal of this section was to cull wolves which had the highest DI, as it represented their risk for depredation, and therefore should be representative of their rate of successful depredation.

When elaborating a management plan by culling, managers have generally to integrate two parameters:

1. The **viability threshold** under which the size of the targeted population (here *Canis lupus*) should not fall below, at the risk of extinction,
2. The **culling quota**, the maximum part of the targeted population which can be culled.

These parameters must be carefully chosen in order to reach the contradictory objectives of the diminution of depredations and of wolf conservation. Consequently, we also had to think about these two parameters for our modelled management by culling.

The viability threshold

The viability threshold is difficult to estimate, as it is relies on a high number of parameters: the parameters relative to the targeted population itself (its size, its growth rate, its structure [*e.g.* its proportion of breeders, its social organisation...], etc...) but also those related to its environment (prey or predator parameters, size of the environment...) [112]. It is hard to predict the fall of a population, because the parameters relative to the species (the targeted one or the ones in relation) are generally not known precisely (but only approximated) and because the rate and amplitude of catastrophes which can temporarily put in jeopardy the targeted population or its resources are hardly if not impossible to predict. Moreover, predicting the fall of a population requires to rely on past data, which may not apply in the future [118].

[112]: Duchamp et al. (2017), *Expertise collective scientifique sur la viabilité et le devenir de la population de loups en France à long terme sous la coordination ONCFS-MNHN de : Guinot-Ghestem M., Haffner P., Marboutin E., Rousset G., Savoure-Soubelet A., Siblet J.P., Trudelle L.*

[118]: Chapron et al. (2012), *Demographic Viability of the Scandinavian Wolf Population*

[118] used different models, more or less adapted to the wolf's species, to determine the viability threshold for the Scandinavian wolf population. They found that if the studied wolf population was stable (growth rate equal to 1), then 400 to 500 wolves would be enough to keep the risk of extinction lower than 10% over 100 years. However, the authors stressed that this was not a robust estimate of the viability threshold. They considered the provided estimate only gave a rough indication of the size of a non-viable population of Scandinavian wolves, but should not be considered as the strict limit between non-viable and viable populations. Yet managers have generally no other option to base their management on, and decide to directly interpret these estimates as the viability threshold. For example, these estimates are used as such to define the French wolf

viability threshold by the authorities in charge of the wolf management [119].

In the USA, the definition of viability relies on numeric and distributional criteria, in other words, on density. These criteria do not rely on a population viability analysis, because the estimates this analysis provides are considered as unreliable for the reasons explained above [241, p. 69850]. For the Western Great Lake wolf population, the Federal Revised Recovery Plan's of the US Fish and Wildlife Service based its definition of a viable, isolated wolf population by the data of the existing and never extirpated population in Minnesota [242, p. 25].

The viability criterion chosen by the authorities is important for wolf management because it determines the intensity with which a management by culling can be applied on a wolf population. If the population is not fulfilling this criterion, the culling is generally prohibited (*e.g.* in the USA [24]) or reduced (*e.g* culling quota of 10-12% in France when the wolf population was estimated under 500 wolves [114]). Fulfilling this criterion, and the culling can be authorised (*e.g.* in the USA [24]) or increased (*e.g* culling quota of 17-21% in France [120]). So this leads to this question: *how in our model, can we determine the viability threshold?*

To match with the method used by the French authorities to manage the wolf population, we decided to rely the viability definition of our modelled population on the number of individuals. In our model, we fixed the carrying capacity at 10 territories or 10 packs. However, the model did not fix a maximum number of individuals, but this number was restrained by the maximum size a pack could reach (used in the *Dispersal* submodel), the *Emigration* and *Mortality* submodels. We estimated the number of wolves in our modelled population $\hat{N}_{pop}$ would approximate 50 wolves once the area colonisation was finished. We obtained this estimate with this formula:

$$\hat{N}_{pop} = (\bar{N}_{indpp} \times N_{cc}) + (\bar{N}_{indpp} \times N_{cc} \times p_{disp}) \tag{2.4}$$

where $\bar{N}_{indpp}$ was the mean number of individuals per pack equal to 4.4 [190], N_{cc} was the maximum number of packs in our model (carrying capacity) equal to 10, and p_{disp} was the estimated proportion of dispersers which did not emigrate, equal to $12/87 = 0.14$ [190]. We considered $\hat{N}_{pop}$ to be an approximation of the maximum amount of wolves that the modelled area could bear, the wolf population stabilising when reaching this estimate (growth rate ~ 1).

Thus, $\hat{N}_{pop}$ is 10 times smaller than the 500 individuals threshold determined earlier. It is normal as the area we modelled was voluntarily small. This meant that confronted to a catastrophe, the risk of extinction was large. However, we did not model any risk of catastrophe in our model (the survival probabilities of adults was high with a short range for standard deviation), as this was not the point of our study. This meant that if our modelled population had colonised most of the modelled area, the risk of extinction was almost non-existent under no management. Now, you could ask me: what do you mean by 'most of the modelled area'? This is the key to our problem here.

In the non-spatially IBM simulating wolf population of [111], the risk

[119]: MTES (2020), *Motif de décision de l'arrêté ministériel du 30 décembre 2019 portant expérimentation de diverses dispositions en matière de dérogations aux interdictions de destruction pouvant être accordées par les préfets concernant le loup (Canis lupus)*

[241]: USFWS (2021), *Endangered and Threatened Wildlife and Plants; Removing the Gray Wolf (Canis Lupus) From the List of Endangered and Threatened Wildlife*

[242]: USFWS (1992), *Recovery Plan for the Eastern Timber Wolf*

[24]: Santiago-Ávila et al. (2020), 'Liberalizing the Killing of Endangered Wolves Was Associated with More Disappearances of Collared Individuals in Wisconsin, USA'

[114]: MTES (2018), *Arrêté Du 19 Février 2018 Fixant Le Nombre Maximum de Spécimens de Loups (Canis Lupus) Dont La Destruction Pourra Être Autorisée Chaque Année*

[120]: MTES (2019), *Arrêté du 26 juillet 2019 portant expérimentation de diverses dispositions en matière de dérogations aux interdictions de destruction pouvant être accordées par les préfets concernant le loup (Canis lupus)*

[111]: Chapron et al. (2003), 'Conservation and Control Strategies for the Wolf (Canis Lupus) in Western Europe Based on Demographic Models'

of extinction over 50 years was under 10% (and even 5%) at only 2-3 reproductive packs under their scenario 3, the closest in terms of adult survival probability to ours. In our model, 3 reproductive packs and the dispersers they created would correspond to ~ 30% of $\hat{N}_{pop}$. However, because the model of [111] and ours, despite being two non-spatial IBM, did not involve the same mechanisms or the same parameter probabilities, we decided not to use the threshold of 30% but to opt for two different definitions for viability threshold: a medium one, at 50% of $\hat{N}_{pop}$, and a high one, at 80% of $\hat{N}_{pop}$. For comparison purposes, we also tested an absence of viability threshold when defining management, meaning that the culling applied regardless of the state of the wolf population.

The culling quota

When modelling the culling component, we had to answer to two questions: *how many individuals are killed, and when during the modelled time step?*

The culling quota in France is currently defined only with regard to the viability threshold but not to the growth rate: the culling quota was of 10-12% when the viability threshold was not reached [114], and has been raised to 17-21% since the viability threshold has been reached [120]. The quota is a range and not a unique number because it takes into account the diverse types of culling, the most simple one, the 'livestock defence shooting with one shooter', being the only one authorised when the number of culled wolves reaches 19% of the population size.

To match with the current French management, we opted to model a unique culling quota of 20% of the population size. We did not model a range of culling quota to keep the model simple, and also because the diverse types of culling encountered in France were not modelled altogether in the same scenario (see section *The culling scenarios* on the next page).

We could have chosen a smaller quota, as the modelled population is small (and therefore more at risk of extinction than a large one). However, we thought that a smaller culling quota would minimise the effects of culling on the structure and on the depredation levels of the wolf population, making it harder for us to analyse these effects. As said earlier, our IBM was not designed for management purpose (*i.e.* to determine an optimal culling quota in regard to population viability and levels of depredations) but to understand the mechanisms under depredation and its relations with culling. However, to compensate the higher extinction risks engendered by the 20% quota, we decided not to model a minimised culling quota of 10-12% under the viability threshold as it was observed in France. This meant that if the modelled population was under the viability threshold, no culling could be applied.

The IBM was modelled over a time step corresponding to one full year. As the *Mortality* submodel, the *Culling* submodel was applied once during one time step. This meant we could not make the distinction between preventive management happening during winter and reactive management happening during summer as in the modelling of [186]. We also had to choose where to place the *Culling* submodel according to the mortality one: before, within or after it? To answer this question,

[186]: Haight et al. (2002), 'Computer Simulation of Wolf-Removal Strategies for Animal Damage Control'

we referred to [177] who analysed that the harvest of wolves in the Northern Rocky Mountains (NRM) was additive to the natural mortality. We therefore modelled that the *Culling* submodel would be triggered after the *Mortality* submodel in our IBM (*cfr.* Figure 2.14). In short, wolves which were culled would not have died 'anyway' during the considered time step. It is true that harvest (hunting) and culling in the context of livestock protection is not the same thing, therefore the results of [177] could not completely apply here.

[177]: Creel et al. (2010), 'Meta-Analysis of Relationships between Human Offtake, Total Mortality and Population Dynamics of Gray Wolves (Canis Lupus)'

Consequently, this meant that the total mortality probability for adults in our model was a maximum of 18% (mortality not related to culling) + 20% (culling) = 38%. It could be less, as the culled wolves did not necessarily include adults only (see next section). This chosen total mortality could appear too high, as it can be found in several studies that above 35% of total mortality, wolf populations face a large risk of extinction [118] [180]. Yet [177] found for NRM wolves that the highest rate of human harvest allowing wolf population sustainability (growth rate of 1) was 22.4%. One could think that the mortality unrelated to harvest for NRM wolves could have been much lower than the one used in our IBM (18%). It seemed that it was not the case as [159] showed mortality probability of adult of 3 years old in the YNP (which is part of the NRM area but where harvest is prohibited) was higher than 18%, with 21% (95% IC 14-29%).

[180]: Marescot et al. (2012), 'Reducing Matrix Population Models with Application to Social Animal Species'

[159]: Cubaynes et al. (2014), 'Density-Dependent Intraspecific Aggression Regulates Survival in Northern Yellowstone Wolves (Canis Lupus)'

The culling scenarios

Without management, the population of our model was expected to grow exponentially during colonisation. To save computation times, we decided to trigger the management by culling before the end of the colonisation period. But to ensure the population was sufficiently grown to sustain management, we triggered the *Culling* submodel only after the first half of the colonisation period (*cfr.* Figure 2.15).

The management by culling then worked as following. At each time step, a number of wolves equal or less than 20% of the population size was culled, at the unique condition that the viability threshold was reached by the wolf population (*cfr.* Figure 2.15). In other words, if at a time step the population was under 80% or 50% of 50 individuals (depending on the used viability threshold), then the culling submodel did not apply and no wolf was culled. In the specific case where the viability threshold was equal to 0, then there is no condition for culling which applied at every time step of the model once the first half of the colonisation period had ended.

In addition to the scenarios on the wolf depredation behaviour, we decided to test the effects of two different culling strategies (*cfr.* Figure 2.15), which did not differ in the number of culled wolves, but on their identities.

- **Culling is oriented towards depredating wolves (H_1).** This hypothesis mimicked the 'defence shootings' in France, where only wolves in position of depredation are culled.
  When the *Culling* submodel triggered, the individuals with a negative DI were excluded from the culling management, because they were considered as avoiding livestock and unlikely to cause depredation. Therefore, they could not be culled.

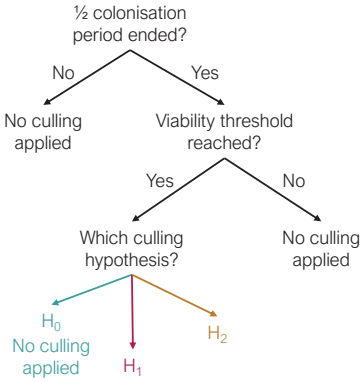

Figure 2.15: The decision tree used in the IBM at each time step when the population entered the *Culling* submodel. The viability threshold could be 50% or 80% of the population size, or null (= 0%), depending on the scenario. The two hypotheses (H_1 and H_2) and the null hypothesis (H_0) referred to the ones of the *Culling* submodel. Credits: O. Grente

For the rest of the individuals (with DI equal or greater than 0), culling was applied individually using a Bernoulli distribution, as in the *Mortality* submodel. The probability used in the Bernoulli distribution for a wolf i was equal to its DI (DI_i):

$$PC_i \sim Bernoulli(DI_i) \tag{2.5}$$

If PC_i was equal to 1, then the wolf i was considered as 'potentially culled'. All the potentially culled wolves were effectively culled if their number was equal or less than the culling quota of 20% of the population size of the time step.
In the case where their number was greater than this quota, then we randomly drew the exact number of wolves allowed by the quota among the potentially culled wolves, each wolves having a drawing probability equal to its DI.
This way, wolves which were the most likely to cause depredation, and above all to reiterate depredations, were the most likely to be culled.

- **Culling is random (H_2).** This hypothesis mimicked the 'hunting shootings' in France, where wolves in areas with high rates of depredation are culled regardless of their age, and aside from depredation situation. These areas are generally less than a 100 km^2 but are highly varying in size depending on the depredation context. These 'hunting shootings' occur during the depredation period (mainly in summer or in early autumn) and are aimed to decrease the number of wolves and so the local food needs of the predator. They are less and less used by the French authorities, in favour of the defence shootings.
  If this hypothesis was selected, all wolves, regardless of their DI, could be culled during the *Culling* submodel. All wolves of the population, pups included, had the same probability to be culled. The number of culled wolves was equal to the number of wolves culled if the hypothesis H_1 would have been applied instead.
  We could have targeted wolves within packs with highest sum of DI, in order to better mimic the condition that the French hunting shootings are taking place in areas with high levels of depredations. However, we considered that our modelled area was already small, making the culling already locally applied. We therefore decided not to include this condition, as it would have involved to define another arbitrary parameter about the targeted packs.

Besides these two culling hypotheses, we added a null hypothesis H_0 where no culling was applied. This meant that in the scenarios integrating H_0 for the culling hypothesis, the *Culling* submodel was never triggered.

Implementation

The combination of the 14 depredation hypotheses and the 3 culling hypotheses (including the null ones) made a total of 135 scenarios to test. When we added the 3 possibilities for the viability threshold, the combinations reached a total of 315 scenarios. This high number of scenarios prevented us to include the scenarios from Chapter 1 regarding the functioning of the wolf population model. This is why we had to focus on one version of the IBM from Chapter 1. Considering literature,

we chose the version M1 (*cfr.* Fig. 1 in [191]) and the pack size of 4.1 to differentiate large and small packs. We chose the medium parameters for the probabilities of adoption and of budding (0.5) in order to keep their influence moderate considering the absence of information in the literature.

[191]: Bauduin et al. (2020), 'An Individual-Based Model to Explore the Impacts of Lesser-Known Social Dynamics on Wolf Populations'

The colonisation period was not known in advance. We estimated it after the first results of the scenarios involving no culling strategy. The population under no culling strategy approximately stabilised from the 100 th time steps at 42.6 individuals on average ($sd = 0.8$)[9]. At half of the colonisation period, at the 50th time step, the population reached on average 35.6 individuals ($sd = 1.2$) (*cfr.* Figure 2.16).

9: Note that this result was a bit lower than $\hat{N}_{pop}$ expected at 50 individuals.

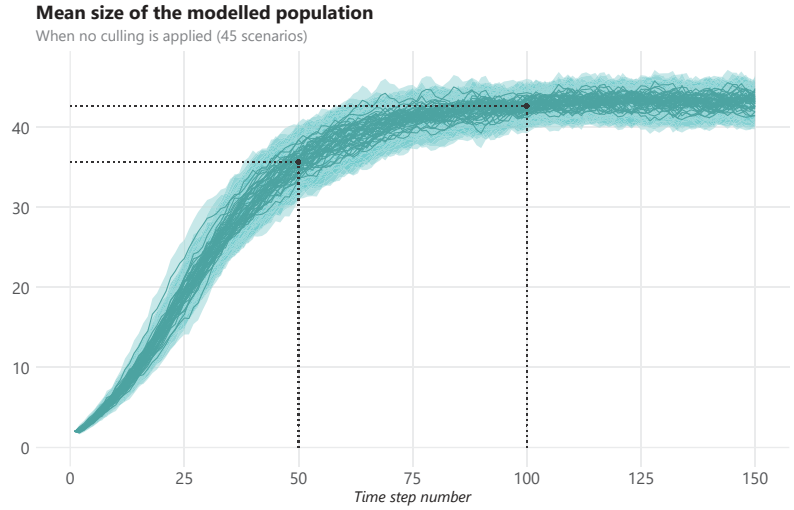

Figure 2.16: Number of wolves of the simulated population following the IBM cycle presented in Figure 2.14 across the 150 computed time steps, for the 45 scenarios with no culling applied (H_0 for culling). Each line represented the mean number of wolves of a scenario (averaged over 150 replicates), and the ribbons represented the 95% confidence interval for normal distribution. One time step represented the full accomplishment of a cycle, simulating the duration of a year. Credits: O. Grente.

As mentioned in section *The culling scenarios*, we triggered the culling submodel after the half of the colonisation period, at the 50th year. In order to get a sufficient hindsight to be able to see all the effects of culling, we opted for running the model for 150 times steps in all (50 years + 100 years of management if any).

Finally, we had to choose the number of replicates, in other words the number of times a scenario would be run (reasons are explained in Appendix B). In Chapter 1, we used 200 replicates, but for a period six times shorter. Therefore, we could use 200 replicates or less. To decide, we computed for 25 randomly-selected scenarios the mean of three parameters (the annual number of individuals, of packs and the annual DI population sum) averaged for 50, 100, 150 and 200 replicates over 150 time steps. Results are provided in Chapter B (The depredation behaviour) on page 287. We found that the means of the parameters averaged over 50 replicates were highly unstable from one time step to another: the influence of extreme simulations were still noticeable. The stabilisation of the means were noticeable from 150 replicates and above. We therefore chose to replicate 150 times each scenario of the IBM model.

The model was coded in R 4.0.2 [193]. As previously, we used the R package *NetLogoR* [194] but switched from the package *pedantics* [195] to the package *kinship2* [243] to calculate with high computational speed relatedness between individuals using their mother and father IDs. We still used the packages *SciViews* [196] for the logarithms functions.

[193]: R Core Team (2020), *R: A Language and Environment for Statistical Computing*

[194]: Bauduin et al. (2019), 'NetLogoR'

[195]: Morrissey (2018), *Pedantics: Functions to Facilitate Power and Sensitivity Analyses for Genetic Studies of Natural Populations*

[243]: Sinnwell et al. (2020), *Kinship2: Pedigree Functions*

[196]: Grosjean (2020), *SciViews-R*

If you haven't read it all you are forgiven

The IBM was modelled as a small area that could be the home of a maximum of 10 wolf packs. We did not model an initial population, and the population built up itself through immigration. Once the colonisation period of the area was half over (without culling), one of two culling management hypotheses applied: a targeted culling of 20% of the population or a random culling of 20% of the population. For comparison purposes, absence of culling was also tested. At each time step, the culling was applied only if the population had reached the viability threshold. Because it was hard to define, we tested three viability thresholds: 80%, 50% or 0% of 50 individuals, which could be seen as scenarios too. **The total number of tested scenarios is therefore 315!**

2.4 Results

It was not possible to analyse the 315 scenarios one by one. I therefore decided to focus on a small range of scenarios (*i.e.* combinations of hypotheses) that were relevant to the PhD.

I divided the results into two parts. The first part focused on the hypotheses regarding the depredation behaviour only, when the second part also included the culling hypotheses.

The three tested hypotheses on depredation behaviour

This first section of the results constitutes a verification phase of the three tested hypotheses about depredation behaviour: (i) about territory knowledge, (ii) about hunting efficiency and (iii) about learning. We intentionally did let aside the effect of culling in this analysis. In short, we only used the scenarios for which the culling hypothesis was H_0. This part intended to check if the population did react the way we expected in response to the hypotheses we modelled about the depredation behaviour.

When the culling component was turned off, the differences between the scenarios in this chapter only applied on the Depredation Index of the individuals, the rest of the population parameters (size, pack numbers etc...) was not affected. In this part, we will therefore focus on the Depredation Index parameter. There was three levels on which the DI had to be summarised:

- *The time step (or year)*: Each wolf of a population in a given time step had an associated DI. To compile the DI at the population level, we had two choices: average or sum the DI of the wolves. We chose to sum them because it summarised two types of information: the inclination towards depredation but also the number of wolves. **The DI sum hence reflected the overall risk of a population to cause depredations.** The DI mean would not have been as informative as the DI sum in that sense[10]. It is true that in this part, the population size is not expected to differ greatly between scenarios as there

10: Imagine two hypothetical populations with the same DI mean of 0.5 (sd = 0), but one with 40 individuals, and the other one with 10. With the first population, there would be 4 times more risks that depredation occurs compared to the second one. With the DI sum, this is an information we caught, as the DI sum would have been 20 in the first population and 5 in the second.

is no culling applied. However, it will in the second part of the results.

- *The replicate*: A replicate was constituted of 150 times steps, each time step having a DI sum. To compile the 150 DI sums of a replicate, we averaged them. However, we chose to average them only from the 50th time steps to the 150th last time step. In other words, we excluded from the mean the first time steps, corresponding to the first half of the colonisation phase. This way, we removed the risks for high variations in the results which were not due to the scenario, but mainly to colonisation.
- *The scenario*: A scenario included 150 replicates. We visualised the 150 means of DI sum of a scenario as a distribution. The corresponding equation is given in Equation 2.6.

$$S_r = \frac{\sum_{t=50}^{150} \left(\sum_{i=1}^{N} DI_{itr} \right)}{100} \tag{2.6}$$

where the blue part of the equation represents the calculations of the *time step* level, with DI_{itr} the value of DI for wolf i during time step t for replicate r. The red part represents the calculations of the *replicate* level. S_r is the final value for replicate r of the scenario, with r going from 1 to 150, as explained in the scenario level.

We analysed the effect on the DI of each depredation hypothesis one by one. For example, the results about the territory knowledge hypothesis included only the scenarios where all the other hypotheses were inactive (*i.e.* H_0 at both individual and pack level). Keep in mind that food intake FI in Equation 2.3, considered as stated, was always included in all scenarios.

The Territory Knowledge hypothesis (i)

As a reminder, the territory knowledge hypothesis was:

- **Individual level:** Wolves living on a long period in the same territory have a higher encounter rate with wild preys, which decreases their depredation risk.
- **Pack level:** Wolves of the same pack are influenced by the territory knowledge of the other pack members concerning wild prey localisations.

The effects on the DI of the territory knowledge hypothesis were analysed with three scenarios, of which the hypotheses are presented in Table 2.5.

Table 2.5: The hypotheses of the three scenarios used to analyse the effect of the territory knowledge hypothesis (i). Results are presented in Figure 2.17.

(a) $H_1(pack)$

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE	✓		
PHE	✓		
IL	✓		
PL	✓		

(b) $H_1(ind.)$

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK	✓		
IHE	✓		
PHE	✓		
IL	✓		
PL	✓		

(c) H_0

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE	✓		
PHE	✓		
IL	✓		
PL	✓		

Results are presented in Figure 2.17. The DI parameter was only dependent on food intake in the third displayed scenario (blue distribution) where all the three hypotheses about depredation behaviour were inactive (Table 2.2 c). Its distribution had a median of 23.8 and was quite large, ranging from 10.5 to 27.7. This meant that some replicates presented a high averaged DI sum because their populations comprised a large

number of large packs, when it was the opposite for the replicates with a low averaged DI sum.

When the territory knowledge hypothesis was active, the DI for each wolf was calculated as the mean between food intake FI (increasing with the number of wolves in the same territory) and territory knowledge TK, as $(FI + TK)/2$. However, the food intake was not expected to differ among the three scenarios of interest here (there is no culling applied), therefore the differences in DI sum distribution between the three displayed scenarios depended mainly on territory knowledge.

As expected, when the hypothesis about territory knowledge was active (purple distributions), the DI was lowered. Indeed, in the scenarios where ITK or PTK were active, the TK decreased the total DI. For example, in the case where an individual had the highest ITK possible, its DI under $H_1(ind.)$ was $(1 - 1)/2 = 0$ and under $H_1(pack)$, it was $(1 - 1 - 1)/3 = -0.33$, where it would have been $1/1 = 1$ under H_0.

The medians of both individual and pack levels did not largely differ, with 11.5 for the individual level ($H_1(ind.)$) and 10.9 when adding the pack level ($H_1(pack)$). The distribution of the averaged DI sum was however slightly more spread out for $H_1(pack)$ than for $H_1(ind.)$, especially because of one outlier among replicates for $H_1(pack)$ with a value at 2.6.

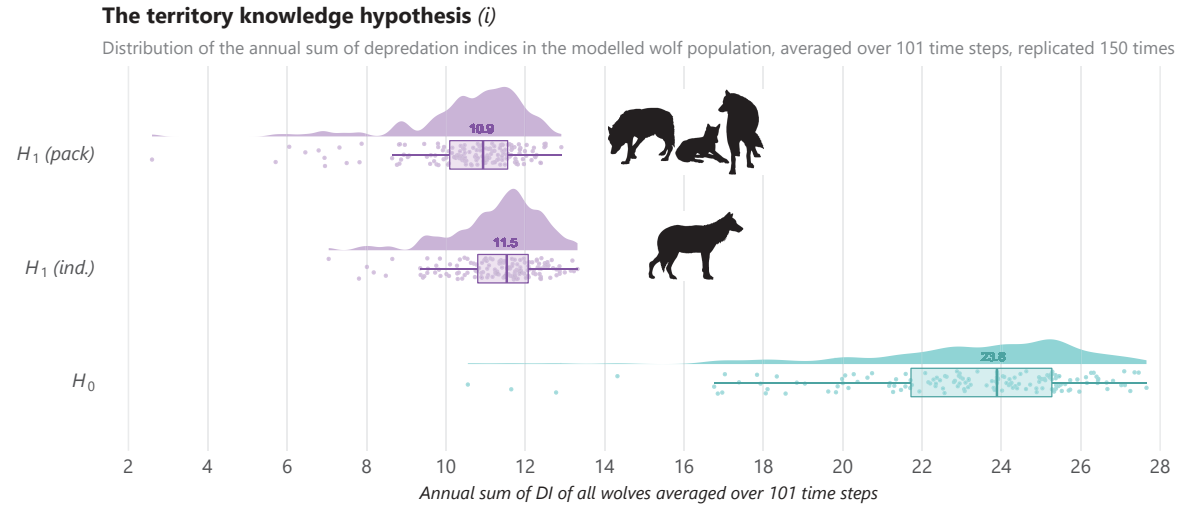

Figure 2.17: Effect of the territory knowledge hypothesis (i) on the DI. Three scenarios are displayed and correspond to the subtables in Table 2.5. For each scenario, each point corresponds to the result of one replicate (S_r in Equation 2.6). This result is the sum of the DI of all the wolves found at a time step of this replicate, averaged over the period ranging from the 50th time step to the 150th time step. There are 150 replicates for each scenario. Credits: O. Grente

The Hunting Efficiency hypothesis (ii)

As a reminder, the hunting efficiency hypothesis was:

- **Individual level:** Adult wolves are more efficient than subadults to hunt. In H_1, the livestock is generally more vulnerable than wild preys, which increases the depredation risks of subadults (because of a lower range of accessible preys). In H_2, the livestock is generally less vulnerable than wild preys, which increases the depredation risks of adults.

- **Pack level:** Larger hunting groups are more efficient than smaller hunting groups to hunt low-vulnerable preys, especially if these groups are composed by adults. In H_1, the livestock is generally more vulnerable than wild preys, which increases the depredation risks of small hunting groups (because of a lower range of accessible preys). In H_2, the livestock is generally less vulnerable than wild preys, which increases the depredation risks of large hunting groups.

The effects on the DI of the hunting efficiency hypothesis were analysed with five scenarios, of which the hypotheses are presented in Table 2.6.

Table 2.6: The hypotheses of the five scenarios used to analyse the effect of the hunting efficiency hypothesis (ii). Results are presented in Figure 2.18.

(a) $H_2(pack)$

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE			✓
PHE			✓
IL	✓		
PL	✓		

(b) $H_2(ind.)$

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE			✓
PHE	✓		
IL	✓		
PL	✓		

(c) $H_1(pack)$

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE		✓	
PHE		✓	
IL	✓		
PL	✓		

(d) $H_1(ind.)$

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE		✓	
PHE	✓		
IL	✓		
PL	✓		

(e) H_0

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE	✓		
PHE	✓		
IL	✓		
PL	✓		

Results are presented in Figure 2.18. The fifth displayed scenario (blue distribution) is the same as the third scenario (blue distribution) in the results for the territory knowledge hypothesis (all tested hypotheses in H_0). When the hunting efficiency hypothesis was active, the DI for each wolf was calculated as the mean between food intake FI (increasing with the number of wolves in the same territory) and hunting efficiency HE, as $(FI + HE)/2$. However, the food intake was not expected to differ among the five scenarios of interest here (there is no culling applied), therefore the differences in DI distribution between five displayed scenarios depended mainly on hunting efficiency.

Under $H_1(ind.)$, the hunting efficiency was of -1 for adults, and of 0 for subadults. Under $H_1(pack)$, the hunting efficiency was decreasing with the size of the pack, up to -1 for the largest packs. Therefore, the DI was expected to strongly decrease for adults, and only slightly for subadults. For example, with a food intake of 1, an adult would have a hunting efficiency of -1, and consequently a DI of $(1 - 1)/2 = 0$, when a subadult would have a hunting efficiency of 0, and consequently a DI of $(1 + 0)/2 = 0.5$, where it would have been $1/1 = 1$ under H_0. The same principle applied for packs according to their size, the individuals of the largest ones having the lowest DI at the pack level. It is therefore normal to observe that under H_1, whether it is $H_1(ind.)$ or $H_1(pack)$, the averaged sum of DI was reduced compared to the null scenario (H_0).

Under $H_2(ind.)$, the hunting efficiency was of 1 for adults, and of 0 for subadults. Therefore, for an adult of a pack with food intake equal to 1, its DI would remain at 1 ($(1 + 1)/2 = 1$) like in the null scenario H_0 ($1/1 = 1$, only food intake counts). The subadults of the same pack would have a lower DI equal to 0.5 ($(1 + 0)/2 = 0.5$). Under $H_2(pack)$, the same principle applied: the DI of individuals in large packs would be close to what was observed in H_0. We noticed here that the medians of the distributions under $H_2(ind.)$ and $H_2(pack)$ were only slightly lower than the median under H_0. This meant that the simulated populations were largely filled by adults and large packs, otherwise the differences of medians between H_2 and H_0 would have been more intense.

You can notice that the median of the DI distribution under $H_1(pack)$ was lower than under $H_1(ind.)$, whereas both medians were equal under $H_2(ind.)$ and $H_2(pack)$. It is due to the fact that the adults and large packs contributed a lot the sum of DI compared to subadults or small packs. I will take an example so that it will be easier to understand. Imagine an adult in a large pack, where the food intake is 1. Its DI under $H_1(ind.)$ is $(1 - 1)/2 = 0$, and under $H_1(pack)$ it is $(1 - 1 - 1)/3 = -0.33$, therefore a bit smaller when considering the pack level. However, under H_2, its DI would be $(1 + 1)/2 = 1$, such as under $H_1(pack)$ with $(1 + 1 + 1)/3 = 1$. If subadults or small packs were on the contrary more represented than aduts or large packs, this would have been the opposite: the medians of the individual and pack levels would have been very close under H_1, and different under H_2.

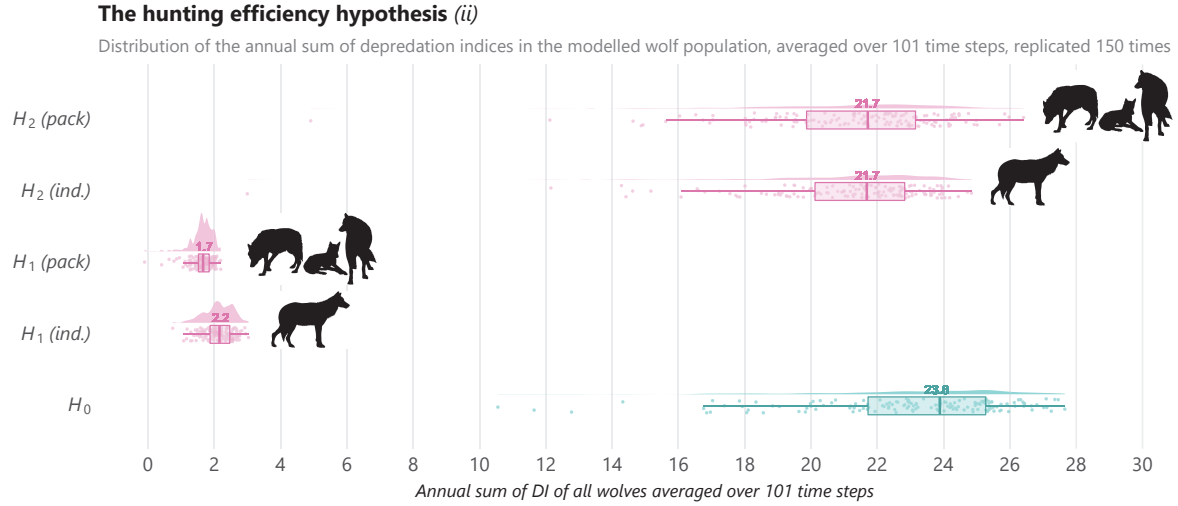

Figure 2.18: Effect of the hunting efficiency hypothesis (ii) on the DI. Five scenarios are displayed and correspond to the subtables in Table 2.6. In H_1, the livestock is generally more vulnerable than wild preys. In H_2, it is the opposite. For each scenario, each point corresponds to result of one replicate (S_r in Equation 2.6). This result is the sum of the DI of all the wolves found at a time step of this replicate, averaged over the period ranging from the 50th time step to the 150th time step. There are 150 replicates for each scenario. Credits: O. Grente

It can appear quite surprising that the overall depredation risk was considerably lower when livestock was more vulnerable (H_1) compared to when it is less vulnerable (H_2). As said in the last paragraphs, this situation was due to the choices during modelling and the prevalence of adults over subadults in the population. This is the reason why it was not possible to directly compare the culling effects between the three hypothesis of hunting efficiency (H_0, H_1 and H_2). **The culling effects should be analysed for each hunting efficiency hypothesis independently from**

each other (*e.g.* is culling efficient to reduce depredation under H_1 for hunting efficiency?).

The Learning hypothesis (iii)

As a reminder, the learning hypothesis was:

- **Individual level:** Some wolves learn to bypass the livestock protection system (positive reinforcement), which increases their depredation risk, when others learn to avoid it (negative reinforcement), which decreases their depredation risk.
- **Pack level:** Breeders can transmit their learnings to each other and to subadults when hunting in groups. Subordinates can influence each other when hunting in groups.

The effects on the DI of the learning hypothesis were analysed with three scenarios, of which the hypotheses are presented in Table 2.7.

Table 2.7: The hypotheses of the three scenarios used to analyse the effect of the learning hypothesis (iii). Results are presented in Figure 2.19.

(a) $H_1(pack)$

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE	✓		
PHE	✓		
IL		✓	
PL		✓	

(b) $H_1(ind.)$

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE	✓		
PHE	✓		
IL		✓	
PL	✓		

(c) H_0

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE	✓		
PHE	✓		
IL	✓		
PL	✓		

Results are presented in Figure 2.19. The third displayed scenario (blue distribution) is the same as the H_0 distributions in the two previous hypotheses about territory knowledge and hunting efficiency.

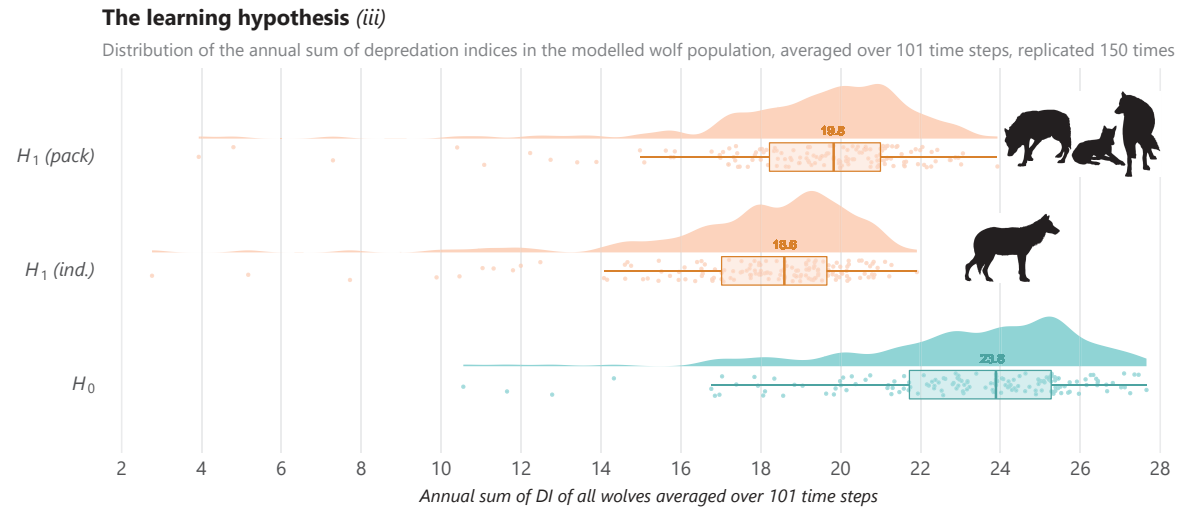

Figure 2.19: Effect of the learning hypothesis (iii) on the DI. Three scenarios are displayed and correspond to the subtables in Table 2.7. For each scenario, each point corresponds to result of one replicate (S_r in Equation 2.6). This result is the sum of the DI of all the wolves found at a time step of this replicate, averaged over the period ranging from the 50th time step to the 150th time step. There are 150 replicates for each scenario. Credits: O. Grente

When the learning hypothesis was active, the DI for each wolf was calculated as the mean between food intake FI (increasing with the

number of wolves in the same territory) and learning L, as $(FI + L)/2$. However, the food intake was not expected to differ among the three displayed scenarios of interest (there is no culling applied), therefore the differences in DI distribution between these scenarios depended mainly on territory knowledge.

When the hypothesis about learning was active (purple distributions), the DI was lowered. We could think that the negative reinforcement was mostly applied, and not the positive reinforcement. However, this was rather due to the way we modelled the DI. Under the scenario H_0 in Table 2.7, the DI was only dependent on food intake, FI (see Equation 2.3). For installed populations as here (we compiled the results after the first half of the colonisation has passed), FI tended to be high because individuals were settled in packs with a breeding pair and offspring. Hence, their DI was high. When averaging FI with learning L under H_1, the DI mostly decreased because L was generally equal or lower to FI in this situation for most of individuals. In a situation where the individuals were not mainly settled in reproductive packs (therefore having $FI << 1$), the activation of the learning hypothesis could have mainly increased the DI for most individuals.

Summary of the first part of results

During this verification phase, we checked how the overall depredation risk of the modelled population reacted to each hypothesis of the depredation behaviour. The territory knowledge decreased the risk for depredation, as expected. The hunting efficiency influenced very differently the DI according to the sub-hypotheses (null, livestock more vulnerable or less vulnerable), mainly because adults were more prevalent in the population than subadults. These three sub-hypotheses should be analysed separately from each other. Finally, the learning abilities reduced the risk for depredation, but we do not expect this result to necessarily maintain under situations for which culling was applied.

The low differences observed between the individual level and the pack level for the three depredation behaviour hypotheses could result from two factors. First, at the pack level, the weights accorded to the individual's and pack's characteristics were equivalent. Second, this result could reflect generally low variabilities among individuals of the same pack for the characteristics used in the DI calculations.

The effects of culling

In this second part of the result analysis, we included the scenarios involving the culling management. This is the long-awaited moment where we will see how the three components from Figure 2.1 interacts: the wolf population component, the depredation component and the culling component.

Rest assured, we did not exhaustively analyse each scenario, or even all the scenarios together[11]. According to the results from the first part, we organised the analysis according to the three very different contexts underlying the hunting efficiency hypothesis: the context where, compared

11: Actually, we have tried, and it was apocalyptic

to most of wild preys, the livestock is as vulnerable, most vulnerable or less vulnerable to wolf's predation. In short, we distinctly treated the three hypotheses H_0, H_1 and H_2 of the hunting efficiency hypothesis.

For each of these three hunting efficiency contexts, the differences between the two types of culling management (the selective one called H_1 and the random one called H_2) and the absence of culling management H_0 were explored.

The results of the three culling scenarios under each hunting efficiency hypothesis were presented following to the same dashboard, constituted by four panels. Each panel represented a parameter directly linked to the general Assumption 1 and Assumption 2 on the culling effect. Schematically, the dashboard can be represented as in Table 2.8. The calculations and visualisation used for each parameter were explained inside their corresponding panels in Table 2.8. The calculations were done independently for each culling scenario. For the Depredation index and disperser rate parameters, the calculations were done from the 50th time step to the 150th last time step for the same reasons as in the first part of the result analysis (in short to decrease the risks for high variations in the results which were not due to the scenarios, but to colonisation).

Except for the population size, the calculations of the three other parameters were done from the 50th time steps to the 150th last time step for

Table 2.8: The schematic representation of the dashboard used to analyse the IBM results. Four parameters were used, each parameter having its own panel. The extraction and visualisation used for each parameter are explained. In the hunting efficiency hypothesis H_0, each panel displays three results, one for each culling scenario. For H_1 and H_2, the panel is divided in two parts: one part representing the results at the individual level, the other part at the pack level.

The **sum of the Depredation Index**.This reflects the depredation level of the population. ► *Extraction for each replicate*: 1. Sum of the DI of all the wolves at each time step. 2. Mean of this sum across the time steps for this replicate. ► *Final visualisation*: Distribution of the means of the DI sum for the 150 replicates.	The **population size**. It is linked to Assumption 1, the decrease in the predator population size assumed to help decreasing the depredation level. ► *Extraction for each replicate*: Number of individuals for each time step. ► *Final visualisation*: Mean of the 150 replicates at each time step, with a 95% Confidence Interval of this mean.
The **pack turnover**. It is linked to Assumption 2, the dislocation of packs assumed to cancel the effects of culling mentioned in Assumption 1, or even to increase the depredation level. ► *Extraction for each replicate*: Maximum number of packs formed from the first time step to the 150th time step, divided by the maximum number of individuals formed from the first time step to the 150th time step. ► *Final visualisation*: Distribution of the maximum number of packs divided by the maximum number of individuals for the 150 replicates.	The **disperser rate**. It is linked to Assumption 2, the proliferation of isolated individuals assumed to cancel the effects of culling mentioned in Assumption 1, or even to increase the depredation level. ► *Extraction for each replicate*: 1. Number of dispersers divided by the total number of individuals at the end of each time step. 2. Mean of this rate across the time steps for this replicate. ► *Final visualisation*: Distribution of the means of the disperser rate for the 150 replicates.

the same reasons as in the first part of the result analysis (in short to decrease the risks for high variations in the results which were not due to the scenarios, but to colonisation).

What about the territory knowledge and learning hypotheses, and the different viability thresholds? We presented here only the figures for which the scenarios considered these hypotheses as true at both the individual and pack levels (*i.e* H_1 (ind.) and H_1 (pack)). Concerning the viability threshold, the figures in this section showed only scenarios with a **viability threshold of 50%**. This meant that the culling managements could only be triggered if the population exceeded $0.5 \times 50 = 25$ individuals after the Reproduction and Mortality components at the beginning of each time step, from the 50th time step (see *The culling component*).

The figures of the results of the other scenarios, considering the territory knowledge and/or learning hypotheses as false at both the individual and pack levels (H_0), or involving no viability threshold (0%) or a viability threshold at 80%, were showed in the appendices. However, their results were still treated in the main text.

Context 0: livestock as vulnerable as wild preys

In this context, livestock are considered as vulnerable as wild preys. If there is no large difference between prey vulnerabilities, then the differences of hunting efficiency amongst wolves are therefore not expected to influence the depredation pattern. In short, whether the wolf is in a large pack or not, whether it is an adult or a subadult, this does not influence its depredation risk in this context.

Let's begin our result analysis by taking the territory knowledge and learning hypotheses as true at both the individual and pack levels. The scenarios considered here are summarised in Table 2.9:

Table 2.9: The three culling scenarios (last line) analysed in Figure 2.20, under the context of H_0 for hunting efficiency.

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE	✓		
PHE	✓		
IL		✓	
PL		✓	
Culling	✓	✓	✓

Results are showed in Figure 2.20. I proceeded to the analysis of the results panel by panel.

Did the culling managements decrease the overall risk for depredation? (Panel A.) *Yes.* The medians of the distributions of the averaged-sum of DI under the selective (H_1) or random (H_2) managements, respectively of 3.8 and 4.3, were lower than the median under no culling (H_0) of 9.9. Only the results of three replicates under H_0 overlapped the distributions from H_1 or H_2. The selective culling was slightly more efficient than the random management to reduce the overall depredation risk.

Did the culling managements reduce the population size? (Panel B.) *Yes.* From the culling triggering at the 50th time step, the means of the annual population size were always lower under culling than under no culling. Both culling managements quickly prevented the population to reach 20 individuals . The population was slightly smaller under the selective culling H_1 than under the random culling H_2.

Did the culling managements cause pack turnover? (Panel C.) *Yes.* The distributions of pack turnover under culling were shifted towards higher values than the distribution of pack turnover without culling and they almost did not overlapped with it. Both culling managements provided

similar distributions of pack turnover but selective culling was linked to a higher median (0.057) than random culling (0.053).

Did the culling managements cause a higher disperser rate? (Panel D.) *No, it was the opposite.* The absence of culling was linked to disperser rates higher than the ones of the scenarios with culling management. The distributions of the annual mean of disperser rate were greatly overlapping between both types of culling managements, but the random culling (H_2) involved generally lower disperser rates than the selective culling (H_1).

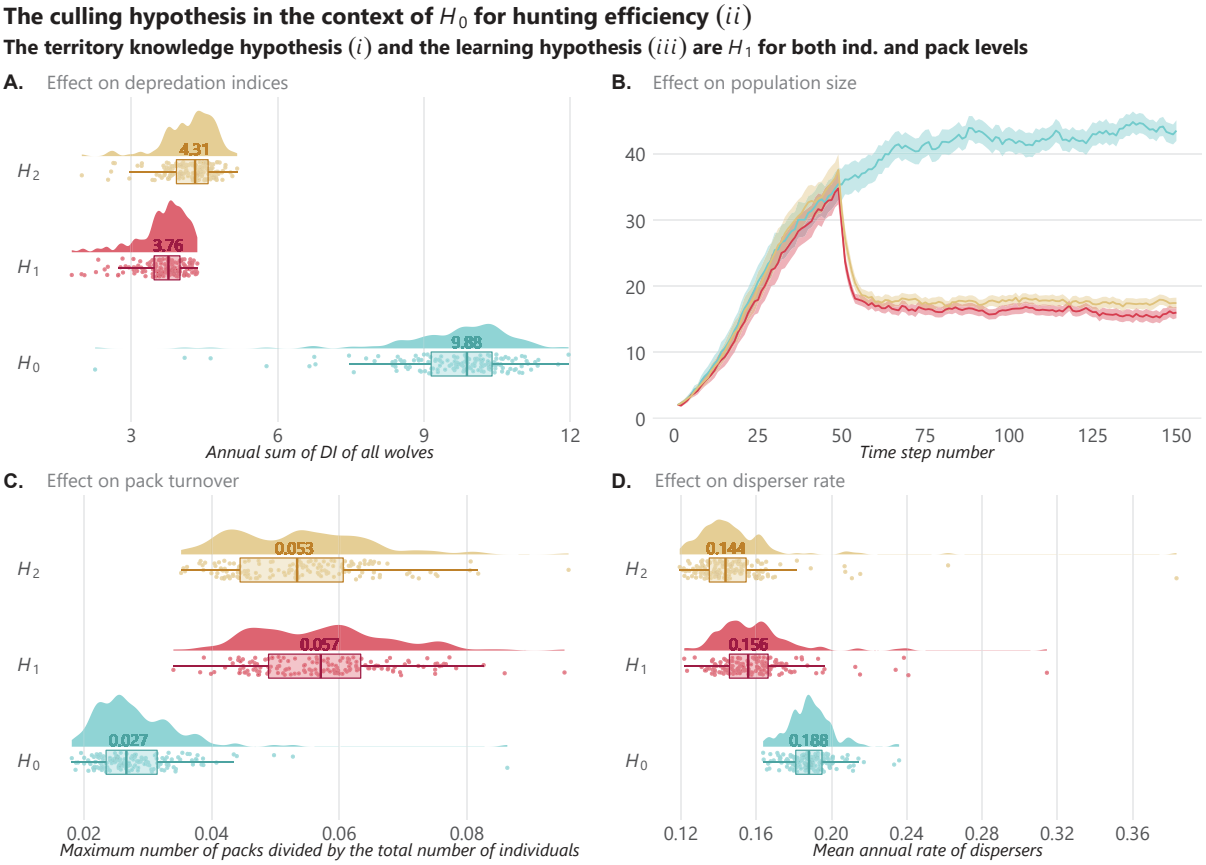

Figure 2.20: Dashboard of the effect of the three different culling managements under the context of H_0 for hunting efficiency, and of H_1 for both territory knowledge and learning (for both individual and pack levels). The blue results refer to an absence of culling management, the red results refer to the selective culling management H_1 and the yellow results refer to the random culling management H_2. The culling managements are explained in *The culling scenarios*. Panels A. and D. reflect the results over the time steps period 50-150. For panel B., the ribbon represents the 95% Confidence Interval of the mean. The visualisation of each parameter is explained in greater detail in Table 2.8. Credits: O. Grente

Let's continue our result analysis, still under context H_0 for hunting efficiency, but taking this time **the other configurations concerning the territory knowledge and learning hypotheses**. We decided to treat simultaneously the individual and pack levels (they are both active or inactive for each hypothesis) as the results in the first part of the results showed that there was no large differences between both levels. Then, the explored configurations were H_0 for both the territory knowledge and learning hypotheses (results presented in Figure B.4a), H_1 for the territory knowledge hypothesis and H_0 for the learning hypothesis (Figure B.4b) and H_0 for the territory knowledge hypothesis and H_1 for the learning hypothesis (Figure B.4c).

The learning hypothesis, whether it was active or not, did not change the

main results previously described in Figure 2.20. Thus, the results from Figure 2.20 and Figure B.4b were very similar.

When the territory knowledge hypothesis was inactive (H_0 in Figure B.4a and Figure B.4c), the values of the averaged DI sums were higher for the three culling scenarios, but there was no changes on the rankings, for any of the four parameters.

What about the results under viability thresholds of 0% or 80%? When considering the exact same scenarios as the ones in Table 2.9, but under these viability thresholds, results were different from Figure 2.20. Figures of these results can be found in the appendices, in Figure B.5.

When allowing wolf culling at any time step from the 50th time step, the efficiency of culling to reduce the overall depredation risks was greater (Figure B.5a Panel A.). However, the cost on the wolf population was too high, as its size never reached 10 individuals a few time steps after culling took place, whether it was under selective or random culling (Panel B.). In this context, the pack turnover was higher with culling than without culling (Panel C.) and the annual disperser rates were very high, especially under selective culling with a median at 48%, against 34% for random culling and 19% without culling (Panel D.).

On the contrary, when the viability threshold was 80% (meaning that the population must be of 40 individuals to allow culling at a time step), the results were closer to those from the same scenarios with viability threshold of 50%. The efficiency to reduce the overall depredation risk in the population was lower than under viability threshold at 50%, but still noticeable (Figure B.5b Panel A.). Population size under culling was higher than what was observed under culling with viability threshold of 50% (Panel B.). Pack turnover was slightly lower under the culling scenarios with 80% for viability threshold, compared to the results with a viability threshold of 50% (Panel C.). No change on disperser rates between these two viability thresholds was however observed.

Context 1: vulnerable livestock

In this context, livestock are considered as more vulnerable than wild preys.Livestock is accessible to wolves regardless their hunting efficiency. However, the range of accessible preys is larger to the most efficient hunters (adults at the individual level, large packs at the pack level). Theoretically, this should decrease the depredation pressure caused by these wolves compared to the one caused by less efficient hunters (see *Hunting efficiency*).

Let's consider again the territory knowledge and learning hypotheses as true at both the individual and pack levels. The scenarios considered here are summarised in Table 2.10. There are six scenarios: three culling scenarios under hunting efficiency H_1 at the individual level only (Table 2.10.a) and the same three culling scenarios under hunting efficiency H_1 at both the individual and pack levels (Table 2.10.b).

Results are showed in Figure 2.21. I proceeded to the analysis of the results panel by panel. The *individual level* and *pack level* on the left and right of each panel refer to the scenarios in Table 2.10.a and Table 2.10.b, respectively.

(a) Individual level

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE		✓	
PHE	✓		
IL		✓	
PL		✓	
Culling	✓	✓	✓

(b) Pack level

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE		✓	
PHE		✓	
IL		✓	
PL		✓	
Culling	✓	✓	✓

Table 2.10: The three culling scenarios (last line) analysed in Figure 2.21, under the context of H_1 for hunting efficiency.

Did the culling managements decrease the overall risk for depredation? (Panel A.) *No.* When hunting efficiency applied at the pack level, the medians of the distributions of the averaged-sum of DI under the selective (H_1) or random (H_2) managements were equal to the median under no culling (H_0). The three distributions were overall very similar. When hunting efficiency applied at the individual level, the random culling provided a distribution overlapping with the one from the scenario without culling (even if the median under the selective culling was lower (0.4) than under the absence of culling (0.8)). The selective culling also provided a lower median than the one without culling, and a distribution shifted towards lower values, but still overlapping with the distribution without culling.

Did the culling managements reduce the population size? (Panel B.) *Yes, but slightly.* From the culling triggering at the 50th time step, the means of the annual population size were always lower under culling than under no culling. However, the difference was clearly less intense compared to the results in the context of H_0 for hunting efficiency. Here, culled populations reached approximately 30 individuals on average, being around 10 individuals less than the scenario without culling, when considering hunting efficiency at the individual level. The difference was even reduced when considering hunting efficiency at the pack level. It was not true for all time steps, but generally the selective culling management caused a lower reduction in population size than the random culling management.

Did the culling managements cause pack turnover? (Panel C.) *Yes, but slightly.* The three distributions of pack turnover overlapped greatly, but the medians were greater under selective culling and random culling than under no culling. The random culling was linked to a slightly higher median value than selective culling, the difference being higher between both medians at the individual level.

Did the culling managements cause a higher disperser rate? (Panel D.) *No, it was the opposite.* The absence of culling was linked to disperser rates higher than the ones of the scenarios with culling management. However, when considering hunting efficiency at the pack level, the differences between scenarios with and without culling reduced, even if the disperser rates remained generally higher under no culling. Both culling strategies provided the same median of disperser rate, and equivalent distributions too.

Let's continue our result analysis, still under context H_1 for hunting efficiency, but taking this time **the other configurations concerning the territory knowledge and learning hypotheses**. As in the previous

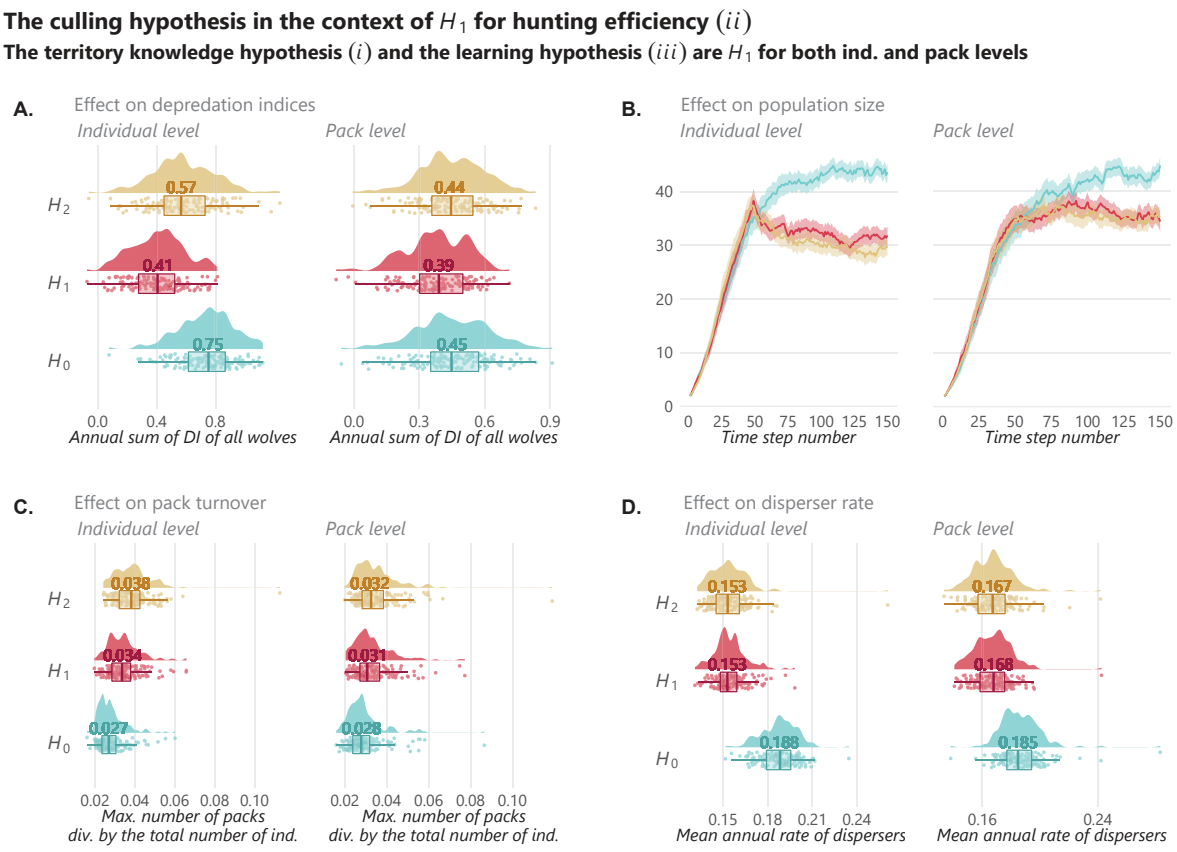

Figure 2.21: Dashboard of the effect of the three different culling managements under the context of of H_1 for hunting efficiency (at the individual level on the left side of the panels, and at the pack level on the right side of the panels), and H_1 for both territory knowledge and learning (individual and pack levels). The blue results refer to an absence of culling management, the red results refer to the selective culling management H_1 and the yellow results refer to the random culling management H_2. The culling managements are explained in *The culling scenarios*. Panels A. and D. reflect the results over the time steps period 50-150. For panel B., the ribbon represents the 95% Confidence Interval of the mean. The visualisation of each parameter is explained in greater detail in Table 2.8. Credits: O. Grente

section, we still treated simultaneously the individual and pack levels for each hypothesis. The explored configurations were H_0 for both the territory knowledge and learning hypotheses (results presented in Figure B.6a), H_1 for the territory knowledge hypothesis and H_0 for the learning hypothesis (Figure B.6b) and H_0 for the territory knowledge hypothesis and H_1 for the learning hypothesis (Figure B.6c).

The learning hypothesis, whether it was active or not, did not change the main results previously described in Figure 2.21. Thus, the results from Figure 2.21 and Figure B.6b were very similar.

On the contrary, the territory knowledge hypothesis did have a greater impact on the results. Both culling managements were more efficient to reduce the DI within the population compared to an absence of culling, if the territory knowledge hypothesis was false (*i.e.* H_0 in Figure B.6a or Figure B.6c). Compared to the context where the territory knowledge hypothesis was true, the two culling strategies reduced more the population size, decreased more the disperser rates and increased more the pack turnover.

What about the results under viability thresholds of 0% or 80%? When considering the exact same scenarios as the ones in Table 2.10, but under

these viability thresholds, results were different from Figure 2.21. Figures of these results can be found in the appendices, in Figure B.7.

There was almost no change noticeable between results of the context 1 (H_1 for hunting efficiency) when modifying the viability threshold, whether it is 0% or 80%. Under 0%, the decrease in the population size over time steps was faster (Figure B.7a Panel A.) than under 50%, and under 80%, this decrease was slower (Figure B.7b Panel A.).

Context 2: highly protected livestock

In this context, livestock are considered as less vulnerable than wild preys. Livestock is accessible to the best hunters amongst wolves (adults or large packs). Therefore, their risk of depredation is increased compared to less efficient hunters in this context.

Let's still consider the territory knowledge and learning hypotheses as true at both the individual and pack levels. The scenarios considered here are summarised in Table 2.11. There are six scenarios: three culling scenarios under H_2 at the individual level only (Table 2.11.a) and the same three culling scenarios under H_2 at both the individual and pack levels (Table 2.11.b).

(a) Individual level

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE			✓
PHE	✓		
IL		✓	
PL		✓	
Culling	✓	✓	✓

(b) Pack level

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE			✓
PHE			✓
IL		✓	
PL		✓	
Culling	✓	✓	✓

Table 2.11: The three culling scenarios (last line) analysed in Figure 2.22, under the context of H_2 for hunting efficiency.

Results are showed in Figure 2.22. I proceeded to the analysis of the results panel by panel. The *individual level* and *pack level* on the left and right of each panel refer to the scenarios in Table 2.11a and Table 2.11.b respectively.

Did the culling managements decrease the overall risk for depredation? (Panel A.) *Yes.* The medians of the distributions of the averaged-sum of DI under the selective (H_1) or random (H_2) managements were lower than the median under no culling (H_0). Only the results of a few replicates under H_0 overlapped the distributions from H_1 or H_2. The selective culling was slightly more efficient than the random management to reduce the overall depredation risk. Results were similar when considering hunting efficiency at the individual or pack levels.

Did the culling managements reduce the population size? (Panel B.) *Yes.* From the culling triggering at the 50th, the means of the annual population size were always lower under culling than without culling. Both culling managements prevented the population to reach 20 individuals. The population was slightly smaller under the selective culling H_1 than under the random culling H_2.Again, results were similar when considering hunting efficiency at the individual or pack levels.

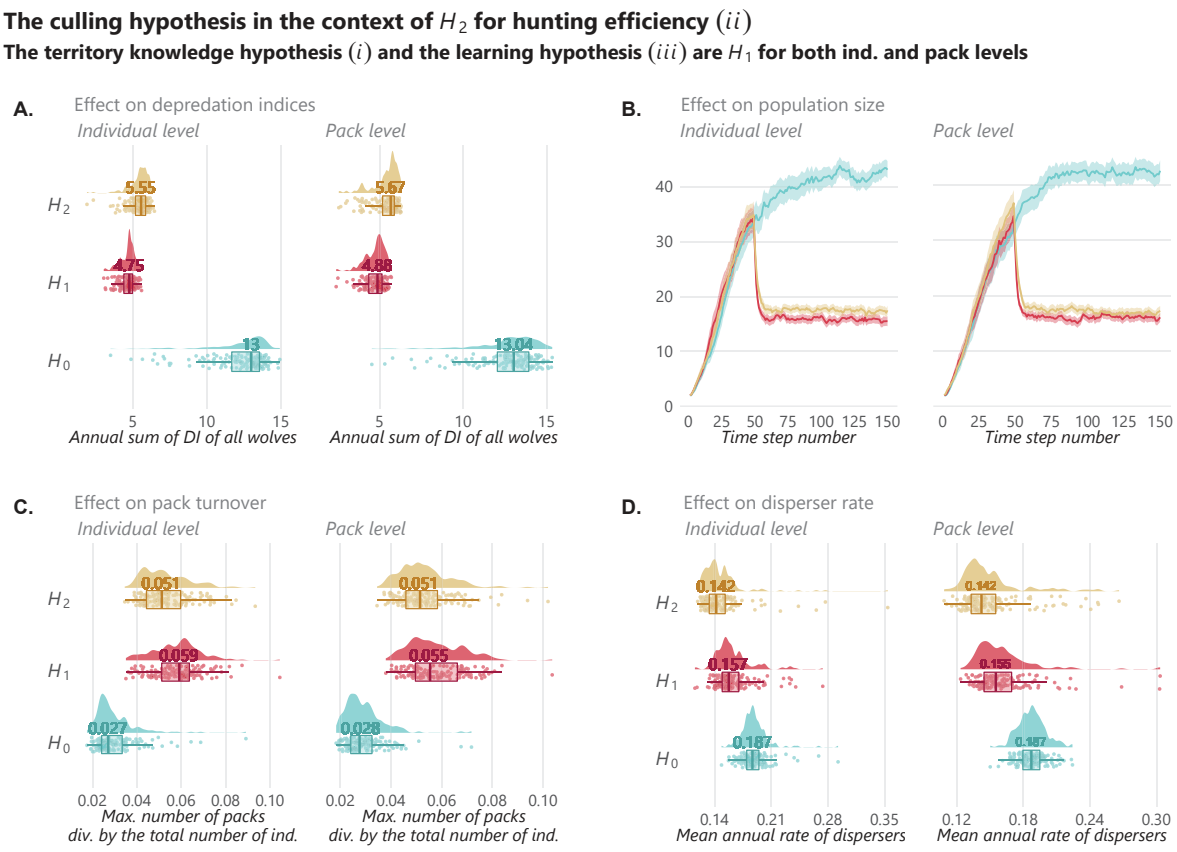

Figure 2.22: Dashboard of the effect of the three different culling managements under the context of H_2 for hunting efficiency (at the individual level on the left side of the panels, and at the pack level on the right side of the panels), and H_1 for both territory knowledge and learning (individual and pack levels). The blue results refer to an absence of culling management, the red results refer to the selective culling management H_1 and the yellow results refer to the random culling management H_2. The culling managements are explained in *The culling scenarios*. Panels A. and D. reflect the results over the time steps period 50-150. For panel B., the ribbon represents the 95% Confidence Interval of the mean. The visualisation of each parameter is explained in greater detail in Table 2.8. Credits: O. Grente

Did the culling managements cause pack turnover? (Panel C.) *Yes.* The distributions of pack turnover under culling were shifted towards higher values than the distribution of pack turnover without culling. The level of overlapping between the distributions under culling on one side, and the distribution without culling on the other side was lower than in the context 1 (hunting efficiency as H_1), but higher than in the context 0 (hunting efficiency as H_0). Both culling managements provided similar distributions of pack turnover but selective culling was linked to a higher median than random culling.

Did the culling managements cause a higher disperser rate? (Panel D.) *No, it was the opposite.* The absence of culling was linked to disperser rates higher than the ones of the scenarios with culling management. Contrary to the previous context (H_1 for hunting efficiency), here the differences between the scenarios with and without culling were equivalent at both the individual level (left side of the panel) and the pack level (right side of the panel). Nonetheless, we noticed that outliers towards high rate of dispersers were more present under culling scenarios at the pack level.

Let's continue our result analysis, still under context H_2 for hunting efficiency, but taking this time **the other configurations concerning the territory knowledge and learning hypotheses**. As in the previous section, we still treated simultaneously the individual and pack levels

for each hypothesis. The configurations explored were H_0 for both the territory knowledge and learning hypotheses (results presented in Figure B.8a), H_1 for the territory knowledge hypothesis and H_0 for the learning hypothesis (Figure B.8b) and H_0 for the territory knowledge hypothesis and H_1 for the learning hypothesis (Figure B.8c).

Again, the learning hypothesis, whether it was active or not, did not change the main results previously described in Figure 2.22. Thus, the results from Figure 2.22 and Figure B.8b were very similar.

Similarly, the territory knowledge hypothesis did not seem to induce large changes compared to the main results previously described in Figure 2.22. Only the distribution of the DI sum seemed slightly impacted by this hypothesis. When territory knowledge hypothesis was considered as false (H_0), the efficiency of the selective or random culling to decrease the depredation risk was more pronounced than when territory knowledge hypothesis was true (H_1).

What about the results under viability thresholds of 0% or 80%? When considering the exact same scenarios as the ones in Table 2.11, but under these viability thresholds, results were different from Figure 2.22. Figures of these results can be found in the appendices, in Figure B.9.

The differences among the three viability thresholds were sensibly equivalent to these observed under context 0 for hunting efficiency. When allowing wolf culling at any time step from the 50th time step, the efficiency of culling to reduce the overall depredation risks was greater (Figure B.9a Panel A.). However, the cost on the wolf population was too high, as its size never reached 10 individuals a few time steps after culling took place, whether it was under selective or random culling (Panel B.). The pack turnover was higher with culling than without culling (Panel C.) and the annual disperser rates were very high, even more under selective culling with a median at the individual level at 63%, against 46% for random culling and 19% without culling (Panel D.).

On the contrary, when the viability threshold was 80% (meaning that the population must be of 40 individuals to allow culling at a time step), the results were closer to those from the same scenarios with viability threshold of 50%. The efficiency to reduce the overall depredation risk in the population was lower than under viability threshold at 50%, but still noticeable (Figure B.9b Panel A.). Population size under culling was higher than what was observed with viability threshold of 50% (Panel B.). Pack turnover was slightly lower under the culling scenarios with 80% for viability threshold, compared to those with a viability threshold of 50% (Panel C.). The disperser rate distribution under selective culling was shifted towards lower values under scenarios with 80% for viability threshold compared to those with 50% for viability threshold.

2.5 Discussion

Summary of the model

In this chapter, we combined the three components essential to understand the effects of culling of wolves on depredations. We added to the modelling of the wolf population biology from Chapter 1 the modelling of the wolf depredation behaviour and of culling. To my knowledge, only [186] modelled these three components altogether, also within a non-spatial Individual-Based Model as ours. In their study, the wolf depredation behaviour was applied at the pack level, all members of a pack assumed to have the same depredation behaviour regardless the individual characteristics :

> *'Packs in farm territories could have 2 states: a tendency for depredation or not, based on wolf behavior in farm territories (Fritts and Mech 1981). The model assumed an annual probability of 20% that packs with no history of depredation in farm territories initiated this activity. [...] All packs with a history of depredation were assumed to maintain that tendency. Each pack with no history of depredation could [also] switch to a tendency for depredation [...] if a dispersing wolf with a tendency for depredation joined the pack [...]. '* [186], p.3.

[186]: Haight et al. (2002), 'Computer Simulation of Wolf-Removal Strategies for Animal Damage Control'

We could have simplified the wolf depredation behaviour of our model as in [186]. Yet the whole point of our study is to **understand the mechanisms of the effect of culling of wolves on depredations, which are very dependent of the wolf depredation behaviour**. We believed the key of the comprehension of the effects of culling of wolves is to integrate the wolf depredation behaviour. Contrary to [186], the aim of our model was not to provide the design of the optimal management of depredation but to understand how the processes of culling and wolves interacted, in order to give some keys of understanding regarding the two general and opposite assumptions about the culling effects. We have seen in the literature review of this chapter that there might be a large panel of characteristics that could push wolves to depredate more than others, even within the same environment. We sought to model the wolf depredation behaviour accordingly to our literature review.

Modelling all the possible implications of these characteristics in the wolf depredation behaviour would have been technically possible. But if you have read the whole modelling and results parts of this chapter, I assume that you had sometimes as much trouble as we did to navigate through the scenarios presented in the results. Keep in mind that we presented 29 scenarios in the results, 95 if we included those from the appendix A.2, which is still far from the 405 scenarios that were computed in total. Multiplying the number of scenarios makes it hard to go through the whole analysis.

A model will always be a simplification of the real system observed in the real world [183], and ours is no exception. You could reasonably question the interest of such model. After all, we had no choice but to make generalities about groups of individuals in our model based on their characteristics. This is a process that is criticised when using the same tricks for modelling related to the human sphere [244]. In addition,

[183]: Marion et al. (2008), *An Introduction to Mathematical Modelling*

[244]: O'Neil (2016), *Weapons of Math Destruction: How Big Data Increases Inequality and Threatens Democracy*

our model involved a lot of stochastic processes (more explanations in the appendix *Required minimum number of replicates*), in short based on probabilities, in contrast to deterministic processes where the outcomes are fixed for the same starting points [183]. In philosophical sciences, the principle of stochasticity can questioned, and viewed as a way to compensate our lack of comprehension of a mechanism[12]. In our model, the number of pups produced by a breeding pair is stochastic (the number is not known in advance). In the wild, this number could be completely determined by some processes (health of the mother? prey density? climate?...), but because this is totally unknown to us, reproduction appears like a stochastic process.

12: *'If we call on probabilities, it is by lack of awareness of fine details which drive the evolution of a system.'*, Etienne Klein, at the Global Congress on randomness, Conservatoire national des arts et métiers, Paris, France, 1st July 2021. The talk is available here.

Consequently, as in every study relying on modelling, we had to find a balance between simplification and complexity for our model. We decided to focus the modelling of the wolf depredation behaviour at the individual scale on four hypotheses from the literature review: the food needs, the territory knowledge, the learning abilities and the hunting efficiency. We selected these hypotheses because of their support in the literature review and/or because they were involved in Assumption 2. We did not include more hypotheses essentially to keep the model results readable. We also stated the hypothesis regarding food needs as always true in our model, in order to decrease the number of scenarios in the analysis.

Interpretation of the results

According to Assumption 1, culling has the effect to reduce the depredation level by reducing the number of wolves. According to Assumption 2, culling has the effect to increase the depredation level by causing isolated individuals.

None of the three contexts reflecting the levels of livestock vulnerability was associated with a depredation level increased by culling. In the case where the livestock is as vulnerable as wild preys (context 0), or less vulnerable than wild preys (context 2), culling was associated with a decrease of the population depredation level, therefore confirming Assumption 1. However, in the case where the livestock is more vulnerable than wild preys (context 1), culling had not a noticeable effect on depredation levels, therefore leaning towards Assumption 2.

What were the mechanisms responsible for these results? The main mechanism underlying the reduction of the depredation level in contexts 0 and 2 was the reduction in population size, as predicted in Assumption 1. This was confirmed by the results when the viability threshold was increased to 80%: by preventing the culling of more individuals, a larger population is allowed which in turn makes the culling less efficient to reduce the overall depredation level.

In the contexts 0 and 2, culling was also linked to more pack turnover, as predicted in Assumption 2. In context 2, this could be explained by the fact that adults were modelled to be more inclined to depredations, and therefore more targeted by selective culling. Some culled adults being breeders, the scenarios with selective culling involved higher rates of pack dissolutions. In this specific context, pack dissolution could actually help to decrease the depredation level if wolves can only successfully

depredate in groups. This is however not verified in our results, as the depredation level was even slightly higher under the context 2 when the hunting efficiency hypothesis was activated at the pack level.

However, we could wonder why random culling in context 2 produced as much pack turnover as selective culling in both context 0 and 2? Yet, in random culling, adults or members of large packs were not more targeted than others by culling contrary to the selective culling under context 2. This can be explained by the prevalence of adults within the modelled population (as seen in the first part of the result analysis). Because culling was modelled as an additive mortality, the higher risks of natural mortality of pups and subadults was happening before culling in our model, therefore increasing the ratio of adults within the population at the time when the culling component was applied. Thus, whether it is context 0 or 2, and selective or random culling, adults were predominantly culled, resulting in an increased risk for pack turnover.

Surprisingly, the disperser rates decreased within the population when culling was applied in both contexts 0 and 2, contrary to the expectations of Assumption 2.For the selective culling under context 2, this is surprising because the dispersers were not preferentially targeted by culling, as their hunting efficiency was low (such as their territory knowledge in the case when this hypothesis was activated as in Figure 2.22). In context 2, the rates of dispersers under selective culling was indeed higher than the rate under random culling (confirming that dispersers were selectively less culled), but both disperser rates were still lower than without culling. The reasons for this result were multiple. The culling of a large number of adults could 'release a seat' in a pack for a disperser, therefore allowing it to become resident. In addition, culling of adult residents could postpone reproduction, and therefore reduce the number of pups in a pack, therefore increasing the chance for adoption and thus to become a resident for young dispersers. Finally, the postponing of reproduction was eventually decreasing the number of pups produced, and therefore of dispersers in the following steps.

Thus, the number of dispersers could actually decrease because of culling instead of increasing. Contrary to what is expected, a lower rate of dispersers (here 14-16% under culling against 19% without culling) could therefore be a bad signal for wolf conservation. The presence of dispersers is normal in a healthy wolf population. In [31], p.11, wolf pack is depicted as a '*dispersal pump*'. However, a too high disperser rate could equally be a bad signal for wolf conservation. When using no restriction for culling in contexts 0 and 2 (viability thresholds at 0%), the population crashed, and the disperser rates were very high, with dispersers sometimes representing more than half of the population.

With culling associated to lower depredation levels and disperser rates in contexts 0 and 2, this challenges Assumption 2, which predicted the exact opposite. However, in these contexts, lone individuals were not more inclined to depredate, contrary to context 1. So culling efficiency could have been different under context 1. In this specific context, culling was indeed poorly efficient to reduce the overall depredation risk of a population. However, contrary to the prediction of Assumption 2, this seemed not to be explained by culling causing more dispersers, as the

disperser rates were actually lower in the scenarios of context 1 with culling than those without culling.

As previously, the culling effect on depredation level seemed rather explained by population size, and in this case by the low reduction in population size. This was again due to the prevalence of adults in packs in the population. In this context, especially with the territory knowledge hypothesis activated, their DI was low and negative. Therefore, they could not be culled, and the number of individuals with a positive DI was low, involving a low number of culled wolves in both selective and random culling (the number of culled wolves in random culling was directly dependent on the one in the selective culling). This configuration caused a population almost unaffected by culling, explaining why the results with or without culling were very close for the four parameters (Figure 2.21).

Thus, if low efficient hunters were more inclined to depredation in context 1, selective culling did not effectively reduce the depredation level because it was already very low. It is not possible to conclude about random culling here: even if any wolf could be culled with this type of culling, the number of culled wolves (imposed by the configuration under selective culling) was too low to observe the effects of culling. Making culling more flexible by suppressing the condition for viability threshold did not increase the efficiency of selective culling efficiency (B.7a), confirming that only a low number of wolves attacked under this context (as attested by the medians of the DI sum distributions close to 0). Thus, the use of culling was useless in context 1 with this kind of population where adults in packs are predominant when culling was applied.

A French scenario?

We could wonder if there is, amongst the scenarios we have tested in this chapter, a scenario that is close to what is observed in France. In our country, sheep represent 90% of the livestock depredated by wolves [71]. Depredation occurs mainly in summer up to autumn for most of pastures because grazing sheep are numerous during this period, due to the *transhumance* practice in the Alps. Therefore, the period of depredation mainly overlap with the period of the *rendez-vous* sites for wolves,when the breeding pair has to feed its pups restricted to a specific place within the territory.

In France, the observations of IPRA and the information gathered by CERPAM seemed to agree on a form of ability from wolves to learn how to exploit the habits of flocks or weaknesses of their protection systems. Moreover, the pastoral activities involved that flocks have no an homogeneous level of protection through the day. During the night, they are easily protected because they are gathered and generally under the protection of dogs. But during the day, they are spread in sometimes large pastures, and can also be less easy to watch for dogs during moves at dusk and dawn between the place where they stay at night and the pasture. Here, experience could be of particular interest for wolves and play a role in the success of their attempts of depredations. The switch observed from night to day attacks goes in this direction. There is however still

little information regarding the transmission of this knowledge among wolves when focusing only on France.

Concerning the territory knowledge, it is hard to say, as we have seen in the literature review. There is no information at the individual scale available to evaluate if the territory knowledge has an influence, positive or negative, on the depredation risk. At the population level, the most attacked flocks are not located in the new colonisation zones, but rather in the south-east of the country, notably in the Mercantour National Park where wolves first re-established after their extinction from France. The depredation distribution is explained in more details in Chapter 4. This could suppose that the territory knowledge as formulated previously does not apply in France, or even increase depredation risks. However, it is not possible to conclude at the individual level for sure only based on information at the population level.

By contrast, points of view disagree regarding the hypothesis of hunting efficiency at the individual level. The most important and reliable source of information is the records of wolves killed from livestock defence culling. From 2011 to 2020, only 31/240 = 13% of wolves culled near flocks were not qualified as adults in France. Therefore, it seems that adults are apparently more wandering around flocks and more familiar with depredation than subadults or pups. This could be relative to the wolf predation behaviour. For pups, it is quite admitted that they do not hunt before their first autumn at the earliest. For subadults, they could actively avoid livestock, being a possible explanation for why so few of them are culled near pastures. However, this contradicts [237] where they have the perception to observe subadults wandering around livestock, maybe more than breeders, but the distinction of wolves of these age classes is extremely difficult, even more at long distance. Maybe the distinction between ages during the autopsies of the culled wolves is also not sufficiently advanced to allow a real distinction of subadults and adults[13]. Arguably, there is still the possibility that in some areas, subadults may be equally or more inclined to depredation than adults from their territory, but because they are not efficient hunters yet, they do rarely succeed in depredation, explaining why they are less culled[14]. Ultimately, a reason for seeing more adults than subadults in the culling records in France could simply be due to a prevalence of adults in the population compared to subadults, as in our model. After all, the subadult class concerns only wolves in their 2nd year, when the adult class has no upper limits of age.

13: A work is in progress at the OFB to improve the age recognition of dead wolves based on the use of their teeth.

14: Currently, most wolves are killed during reinforced livestock defence culling, applied for flocks with at least 3 successful and verified depredations

Similarly, there is not a consensus related to the size of hunting groups related to depredation, in short concerning the hypothesis of hunting efficiency at the pack level. Several sources of observation ([232], *brigadiers*) related that wolves were mainly seen alone when approaching or attacking flocks, in several environmental and pastoral contexts. This contrasts with pastoral information from CERPAM that mentioned frequent attacks from wolves in groups in the same contexts as those where IPRA and the *brigadiers* have made their observations. Maybe the inconsistency originated from the fact that IPRA and the *brigadiers* were posted around livestock for a large numbers of nights, therefore including the nights where wolves alone or by two approached flocks without necessarily succeeding in the attacks. The attempts of attacks by wolves alone or by two do not prevent that a larger number of wolves could attack altogether

[232]: Landry et al. (2020), 'Interactions between Livestock Guarding Dogs and Wolves in the Southern French Alps'

at other times, where the risk for a successful attack is higher. This would be consistent with the observations of IPRA [153] where wolves of the same pack in summer were mainly seen leaving the *rendez-vous* site separately, but sometimes were seen leaving altogether, and in this case were generally splitting up at some point during the night (as mentioned by S. Rigeade too). This tactics seems to reflect that it was more profitable for wolves to separately hunt in France, because the hunted preys did not require a large number of wolves to be killed (contrary to bisons in the YNP [207] or elk in Scandinavia [212]) and killing them alone or only by two increased the food intake for these wolves. In short, wolves in summer in south-east France might split up to increase the chances to encounter, surprise and kill what are probably small wild preys. As shown by several studies, wolves in France tend to eat indeed small preys compared to other areas: chamois and roe deer for wild preys, showing low rate for wild boars or red deer [221]. It would be interesting to know if this behaviour is maintained in an equivalent environmental context where there is no flock, or during a summer where flocks did not use the pastures. Hence, it would be possible to know if this hunting behaviour occurring in summer is due to wild preys or livestock.

So in France it seems that wolves have higher chances to encounter livestock alone (or at least not in large hunting groups). However, I would like to highlight two important points that can be sources of misinterpretation here.

1. **We should not confuse a wolf wandering or hunting alone with a wolf in dispersion or a lone wolf** (*i.e.* territorial wolf without any pack member).

It is easy, when seeing videos of wolves attacking livestock alone, to hastily conclude that these wolves are loners which have no choice but to attack livestock, supposedly more accessible than wild preys, whereas they could have attacked wild preys if they have been in a pack. To me, this mistake is reinforced by the common portrayals in TV documentaries of large packs of wolves hunting large preys in North America, as I explained in the literature review.

In France, a large panel of preys are available, from small (e.g. rodents), medium (e.g. roe deer) to large (e.g. red deer). Contrary to North America as in the open spaces of Alaska or Canada, wolves in France have no vital need to form large hunting groups to feed, because small or medium preys would always be easily accessible in forested areas. As observed by IPRA in [153], wolves in France could be mostly solitary hunters, at least in summer, even if they are part of a pack with several members of hunting age.

It is true that wolves in large packs have a bigger panel of accessible preys, as they can easily target larger preys compared to loners [208]. In Vercors, France, [245] showed that in winter wolves tended to feed more on red deer than roe deer with time, possibly because of increases in pack sizes. These studies suggest that wolves in large pack adapt their diet to the increased food needs, notably by taking advantage of their higher hunting efficiency in group. However, by no mean this suggests that wolves in France seek to form large packs in order to feed on large preys, as medium preys are available. Wolves in Vercors still feed on roe

[245]: Randon et al. (2020), 'Population Responses of Roe Deer to the Recolonization of the French Vercors by Wolves'

deer for example [245], suggesting that solitary hunting, even if packs are larger, is probably still existing, even in winter.

It is then important to keep in mind that the life of wolves in pack is not always due to the need to hunt in groups. Wolves can live in packs in order to better defend their territory or increase their reproductive success [158].

[158]: Ausband et al. (2021), 'The Effect of Group Size on Reproduction in Cooperatively Breeding Gray Wolves Depends on Density'

2. **Attacks of wolves do not always succeed.**

As any predator, all attempts to kill a prey do not end in success, and sometimes most of them end in failures. Wolves are no exception, with hunting success rates of elk and roe deer in Scandinavia of 43% and 47% respectively [215]. Predation on livestock is no different. Around 71% of wolf attacks on livestock were failures in a study in France [232].

However, the failed attacks are rarely if ever taking into account in studies about depredations, including ours. Whether we are a farmer or a scientist, we generally have access to the successful attacks only, through the carcasses of livestock or the presence of livestock remains in wolf's faeces. It is therefore hard to assess if all wolves attempting an attack are a threat for livestock.The characteristics of wolves attempting an attack on livestock could be very different from those of the wolves succeeding an attack on livestock. Therefore, it is not because most wolves are seen approaching flocks alone, that they are the wolves which succeed in depredation.

This lead us to the final point of this section. As we have seen in the literature review, the success of attack of wolves depends on the prey vulnerability. For livestock, the intrinsic vulnerability mainly depends on their level of protection [224]. This is what seemed to play a role in the very low depredation success of wolves in [232]: the flocks were protected by livestock guarding dogs of which the interactions with wolves were statistically linked to more attack failures.

However, what happens when flocks in an area are all highly protected? In France, the level of protection in the Alpine range is now overall high for a major part of the area according to [71]. Therefore, this seems to be close to what we have called 'context 2' in our model, where livestock is less vulnerable than most of wild preys in an area. In this context, the individuals with the highest hunting efficiency were preferentially targeted by selective culling in our model, as they were the only ones able to successfully kill livestock (because they are adults, or in large packs).

This scenario would be consistent with the observations from CERPAM where large packs could be more involved in successful depredations, and that this pressure from large packs seems to increase through time (L. Garde, pers. com.). Let's briefly talk about the wolf population in the Alpine range or at proximity. The wolf pack distribution in this extended area is becoming more dense year after year [29] and camera-trap films of large packs appeared these last few years[15]. Establishment opportunities on nearby but free territory is decreasing for young wolves born in dense area [179], therefore decreasing their chances for successful dispersal. Wolves are known to made pre-dispersal excursions before completely leaving their natal pack [31, 35] [173], and in the current situation in the Alps, where the gaps are all closing with new packs, the

15: *e.g.* videos of packs of at least 6 wolves in winter, 8 wolves in spring, or even 13 wolves in fall

[179]: Wikenros et al. (2021), 'Age at First Reproduction in Wolves'

[173]: Messier (1985), 'Solitary Living and Extraterritorial Movements of Wolves in Relation to Social Status and Prey Abundance'

lack of opportunities to establish may push young wolves to stay in their pack. Meanwhile, the need for packs to have a large size to defend their territories against neighbouring packs, that are settling closer than before, is probably increasing too [160]. In the end, packs are probably getting bigger with time in the Alpine range, as it has been showed during wolf recolonisation in North America [31].

[160]: Cassidy et al. (2015), 'Group Composition Effects on Aggressive Interpack Interactions of Gray Wolves in Yellowstone National Park'

Thus, the wolf population situation in the Alpine range is corroborating the possibility that the number of hunts in large pack increased. This does not remove the fact that solitary hunting is still possible, as said above, consistently with the observations made by IPRA or by *brigadiers*. However, because livestock is now protected within most part of the Alpine range, the success of depredation for solitary hunting wolves should be decreasing. All this information tends to confirm that the scenario in France should be close to the modelled 'context 2'.

However, in our model, the context 2 implied that the better hunters (adults or in large packs) were more inclined to depredations, and therefore more targeted by selective culling. In the French scenario as it seems to be, there is no evidence that individuals in large packs are *more inclined* to depredations, only that they could be *more successful* to it. Thus, many wolves hunting alone (whether they are part of large packs or not), can still attempt depredations even in the presence of livestock guarding dogs, as shown by IPRA or *brigadiers*. In addition, we have seen throughout this section that wolves, especially in summer, are mostly seen hunting alone even when part of a pack.Therefore, it is completely possible that the reinforced livestock defence culling is authorised following the successful attacks of large hunting groups, but during the protection operations, mostly wolves hunting alone are seen approaching the flocks, and are culled. However, because of the wolf territoriality, it is highly likely that wolves seen alone around the same flock where the large pack have succeed the attack, would be part of this pack. Hence, context 2 could in the end not be far from the French scenario.

I may disappoint you, but there is 'a fly in the ointment' with this last statement. If the size of hunting groups that attempts depredation may have increased through time in the Alpine range since the beginning of the wolf's recolonisation in France, there is no strong evidence that they succeed more in depredation than wolf hunting alone. It is quite plausible that if an attack of a group of wolves succeeds, it might be more destructive than the successful attack of a wolf hunting alone [64]. However in France, the management of culling is essentially based on the depredation events rather than the number of dead livestock (at least for reinforced defence culling). It is not excluded that wolves hunting alone may cause more depredation events with a lower number of dead livestock than large packs. Even if hunting groups can compete with a high number of livestock guarding dogs, the discretion of wolves hunting alone can favour successful attacks. The results from [232] are also suggesting that it was not the number of wolves or dogs that explained the success of an attack, but rather the number of interactions between them. In short, if a wolf is sufficiently discrete to escape flock and dog's surveillance, it can successfully attack, which is exactly what is happening for the flock of H. Cotton in the Jabron Valley.

There could actually be several contexts corresponding to the French scenario. At high altitude, where flocks are grazing in open areas with low vegetation, dogs can easily monitor their flocks. In this case, it is more context 2 which applies, where large packs are the only ones able to compete with a high number of dogs and to access livestock. Dogs could still not detect the wolves, but sheep gathered as they generally are during nights can rapidly panic and alert the dogs, then disturbing the attacks of wolves. This would correspond to context 2 where the hunting efficiency hypothesis is activated at both the individual and pack level.

At lower altitude, in more bushy pastures, it could be an advantage to stay discrete, because it allows wolves to avoid confrontation with dogs. Requiring no coordination between wolves (whether it is during the attack or even before, to travel together up to a flock as a whole), this type of hunting is probably less consuming for wolves. If adults are indeed more inclined to depredation as suggested by the register of culled wolves in France, then this situation would correspond to context 2 but only at the individual level. In the opposite case, this situation would correspond to context 0, where the age of the wolf or the size of its pack is of no importance regarding its propensity to attempt and succeed depredation, as wolves even in packs tend to hunt alone in France. However, we should not forget the food needs which are higher in a large pack, especially for the breeders which have to feed their pups, so even under context 0 where the hunting efficiency has no importance, flocks within pastures overlapping the territory of large packs could be on average under a larger depredation pressure than otherwise.

In comparison, in the large open areas of North America where preys are large and in herds, where ambush is complicated, pack hunting is surely an asset for wolf's survival and not an option as it could be in France. In this scenario, the context of hunting would probably be close to our context 1, where wolves hunting alone have no easy access to large preys and may report to livestock as sheep, especially if they are not well protected.

There is not one single French scenario but probably several

Because the range of preys is large in France, with medium preys, wolves can hunt alone even when in packs. In addition, in the Alpine range, the protection of livestock is now generalised. In open areas as in pastures of high altitude, it is probably becoming harder for wolves hunting alone to succeed in their attempts of depredation contrary to wolves hunting in groups (H_2 at the pack level). In this situation, this seems to suggest that the scenario where high hunting efficiency at the pack level favours successful depredations would be the closest one. However, in more bushy areas, the discretion of wolves hunting alone may be an asset for wolves to succeed their attempts of predation on protected livestock. Therefore, this situation would become closer to the scenario of context 0 where the size of the pack is of no importance regarding depredation, as wolves, whether they are in packs or not, can hunt alone. The context 1 of our model would more likely correspond to large open areas with great preys in herds requiring pack hunting as it could be in the northern parts of North America.

Regarding the collected information, the hypothesis of learning could be true in France. If this is checked, this could mean that adults, which are more experienced, can take advantage of their experience to exploit the weaknesses of the protection system of the flock. In this case, the hunting efficiency hypothesis H_2 at the individual level could applied in both open and closed areas. The last hypothesis regarding territory knowledge is the one where there is the greater lack of information, and where no conclusions can be suggested in France.

Enhancements and limits of the study

Our study was not free from limits, and there were numerous. We list here some of them, with some proposals to enhance the model or future IBMs on wolf depredation behaviour.

The main limit of our study is the limited amount of tested hypotheses. We have seen that we let aside a large number of hypotheses from the literature review (section *The tested hypotheses*), in order to find a balance between simplification and complexity for our model. There was other relevant hypotheses that could have been tested too.

Moreover, we conditioned the application of an hypothesis at the pack level on the application of this hypothesis at the individual level. This could have been problematic for two reasons. First, we chose that the individual and pack characteristics would have the same weight on the DI. However, the influences of this two levels of characteristics could have been unbalanced when both coexisted for the DI calculations. A modelled unbalanced weight could have increased the differences observed between both individual and pack levels in the results. Second, the pack level could also have been applied alone in the DI calculations, without necessarily having the need to be applied at the individual level. In particular I have in mind the hunting efficiency hypothesis. We have seen in section *A French scenario?* that the possibility to pack hunting could be important to succeed depredations in some situations in France, whereas the age of the individuals seemed of minor influence. In this case, it could have been interesting to test the hunting efficiency at the pack level without testing it at the individual level.

The modelling of some hypotheses could have been done differently too. The differences between H_1 and H_2 of the hunting efficiency hypothesis were due to the modelling choices to attribute the same value to subadults in both hypotheses (0.5) and to attribute opposite values for adults (-1 for H_1 and +1 for H_2). The idea was to penalise adults in H_1 and to favour them in H_2 by keeping subadults as the point of reference in both contexts. In retrospect, I think that it would have been easier to compare both contexts of hunting efficiency if we had attributed the exact same values in both hypotheses, but by inverting the age classes: for example, 0.5 and 1 for adults and subadults respectively in H_1, and 1 and 0.5 for subadults and adults respectively in H_2.

The learning hypothesis was to my opinion the most poorly modelling hypothesis that we tested. The chosen modelling was suppose to reinforce the DI in a way or the other, but I have no choice but to note that it did not work, as the learning hypothesis had almost no influence on any

of the results. A different modelling choice could have been attempted, such as introducing positive or negative events regarding depredation. The learning characteristic was the one designed to create the most individualities, contrary to the other hypotheses which rather grouped individuals according to discrete characteristics (such as age). This is why the learning hypothesis was of special interest, especially in an IBM. When I met J.M. Landry and J.-L. Borelli from IPRA, they insisted that, to them, wolves had their personalities which was probably one of the most explicative factors regarding depredation. A special interest should therefore be deserved to individualities in next modelling of wolf depredation behaviour.

A different modelling of alternative culling hypothesis H_2 could have been tested too. For example, we could allow the random culling to have a number of culled wolves independent from the selective culling. It would have been particularly useful in context 1 (hunting efficiency of H_1) where in our results, the selective culling involved a very low number of culled wolves because of the prevalence of adults.

All the values ranging from -1 to 1 for our hypotheses (Table 2.1) could have been modified (even if keeping them within the range $[-1;1]$), and should have been tested in a sensitivity analysis.

The final point of this section concerns a point raised in the previous section *A French scenario?*. Our IBM was designed to identify the individuals the most *inclined* to depredation. However, in France and probably in other countries as well, it is not the inclination towards depredation which triggers culling, but the *success* in depredation. There could therefore be a discrepancy between the DI and the risks for wolves to be culled, contrary to what was model in our IBM. This is a point that has to be thoroughly examined in future IBMs on wolf depredation behaviour if the culling component is tested.

2.6 Conclusion

Chapter 2: The depredation behaviour

The hunting behaviour of wolves is complex. It depends on the interactions of the three main processes that we have seen in the literature review: food intake, vulnerability of prey and encounter rates. It is highly dependent on the panel of available preys, whether they are wild or domestic.

Besides its complexity, there are still many unknowns regarding the wolf depredation behaviour. Yet, the understanding of this behaviour, whether it concerns predation on wild or domestic animals, is fundamental when studying the effects of lethal removal on the depredation levels. Indeed, according to one's belief in the wolf predation behaviour, one of the two assumptions about culling efficiency will prevail on the other. Whereas **in most cases, there is simply not enough information about the wolf predation behaviour to disentangle these two assumptions**.

In this study, we modelled the predation behaviour of wolves mainly through three tested hypotheses. We could have modelled more hypotheses, or different ones. The point was **not** to provide a management tool able to produce the optimal number of wolves that could be culled without causing population crash or disruptions. **The point was to explore at a local scale the effects of lethal removal according to the different hypotheses about wolf depredation behaviour that are advanced by the two polarised assumptions**. The goal was to understand the mechanisms involved at the individual, pack and population levels in grey wolves that could be modified by lethal removal, and how these changes could in turn affect the effects of lethal removals.

We proposed in this chapter an integrated model of wolves, of their depredation behaviour and of lethal removals. We used an individual-based model where each wolf was modelled, in order to increase the realism of the model. We showed that for some hypotheses, lethal removals were efficient to reduce depredations, essentially through population reduction, despite pack disruptions. For other hypotheses, lethal removals had no substantial effects.

In short, we showed that the efficiency of lethal removals to reduce depredation is inherently linked to the wolf predation behaviour. We have seen through a compilation of the data available in France and elsewhere that the wolf predation behaviour can itself be context-dependent. Therefore, **we can already suggest that it is unlikely that there is a unique effect on depredation of the lethal removals, including in France where a lot of different contexts can be present**.

A growing number of reviews [82, 124, 133] advocates for experimental design to study the effects of lethal removals. However, this design is difficult to apply for large predators, and if it is applied, it would likely be limited to a small scale on a short period. **The IBM could become a tool of replication (*in silico*) of experimental studies of wolf culling effects**.

Chapter Three

Effects of culling on depredation 3

3.1 Aim of the chapter

In the last chapter, we have seen that the full understanding of the effects of lethal removals on depredation levels through the changes on the wolf population is tricky and ambitious. The main reason for this is the lack of data we have, especially regarding the depredation behaviour of wolves. To fill this gap, it would be necessary to conduct field studies in local zones where a large amount of data related to wolves and their individual depredation behaviour is collected.

On the other hand, it is possible to study the effects of lethal removals on the depredation levels without studying the effects of lethal removals on the wolf population (Figure 3.1). This approach has already been used. Indeed, lethal measures and depredations with dead livestock are generally well collected data, and France is no exception in this regard. In addition, the increase in the size of both datasets, due to the wolf recolonisation In France and the increasing culling quota, can allow the use of statistics for the analysis. Indeed, to draw a general conclusion about the efficiency of lethal measures, we cannot rely on a few events only.

This leads us to the question of this chapter: **what are the effects of the legal culling applied in France on the observed depredation levels?** To answer this question, we had no choice but to conduct a retrospective study. The reason is that the data we had at our disposal were not part of an experimental study, but were originating from the French public administration in charge of the depredation management. All the studies already conducted on the effects of lethal removals of wolves on depredation in other countries were also retrospective.

It was important to review these retrospective studies. Because there is still no consensus on the effects of lethal removals [133] that comes from theses studies, it was indeed necessary to identify the gaps in their methodology. We attempted for our own study to fill these gaps as much as possible, given the data available to us and the methods that could apply.

To sum up

The main goal of this chapter is to study the effects of the legal culling applied in France on the observed depredation levels, based on the data collected by the French administration. We reviewed the existing studies on the subject, and attempted to fill the gaps that weakened their methodologies as much as we could, given the fact that we worked with retrospective data too (*i.e.* data that are not originating from a controlled scientific protocol).

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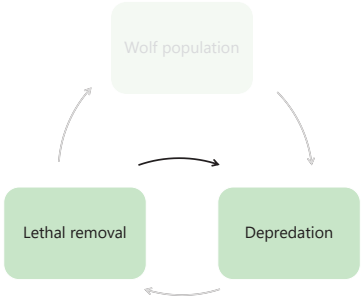


Figure 3.1: Study of the direct effect of lethal removal of wolves on the levels of depredation. Credits: O. Grente

[133]: Treves et al. (2019), 'Predator Control Needs a Standard of Unbiased Randomized Experiments With Cross-Over Design'

3.2 Literature review

Effect of wolf lethal control across the world

There are less than ten studies about the effects of lethal removals of wolves on depredation. All of them focused on North America, except one study on Spain [67]. As mentioned previously, none of them is experimental. They are all retrospective: they use data which is not originating from a scientific protocol. When using retrospective data, there are three analyses possible: the *inter-site comparison*, the *intra-site comparison* or the *correlation*.

[67]: Fernández-Gil et al. (2016), 'Conflict Misleads Large Carnivore Management and Conservation'

Inter-site comparison. The first approach is the closest approach to the experimental design. The approach consists in comparing two groups, one group without treatment (*i.e.* without lethal control) and one group with. However, the choice to protect a flock with lethal removals or not, in other words the distribution of flocks within the two groups, has never been random in the concerned studies by this approach. The choice was always orientated because of management.

Thus, this made the comparison between the two groups complicated and biased. There was a risk for what we call '*confounding factors*'. More explicitly, you could think the effect you observed in the group protected with removals was due to the removals, while it could be due to another variable. In France, if you compare the areas where lethal removals are applied and areas where it is not, you will have a bias regarding the level of depredations, because lethal removals are generally applied in areas of high depredation density. The initial situation regarding depredations between the two groups will therefore be different in France, and could explain the differences of depredations between both groups.

To date, the inter-site comparison has only been used by three studies. The first one is [97] which evaluated the effects of lethal trapping in 434 farms in Minnesota (USA) with data spanning over a period of 20 years. They analysed the delay before the next depredation after a depredation, over the pastoral season (ending in November). They compared this variable between the group of 525 depredations followed by successful trapping with two control groups: the group of 38 depredations where no trapping was implemented after and the group of 360 depredations where trapping was implemented but unsuccessful.

[97]: Harper et al. (2008), 'Effectiveness of Lethal, Directed Wolf-Depredation Control in Minnesota'

They found that only the death of an adult wolf male significantly reduced the depredation recurrence rate at the farm compared to depredations not followed by trapping. When analysing this rate within a 4-km radius around the farm, they found the same result, but they also found that unsuccessful trapping was equally efficient to reduce the depredation recurrence rate. For a 8-km radius around the farm, the trapping, regardless of its success, did not show any effect.

Most of the depredations concerned cattle, but some were on sheep or poultry. When [97] restricted the analysis to farms with depredations on sheep only, they observed that '*there was some evidence that successful trapping led to lower recurrence rates than did no trapping or unsuccessful trapping*'.

The second study to use inter-site comparison is [96] which evaluated the effects of lethal removals in the Northern Rocky Mountains (Montana, Idaho, Wyoming, USA) with data spanning over a period of 22 years. They compared the number of days before the next depredation between 3 groups of depredations: *a)* 593 depredations for which no removal was applied before the next depredation if any, *b)* 326 depredations for which a partial removal of the pack causing the given depredation was applied, with on average 2.2 wolves removed, and *c)* 48 depredations for which a total removal of the pack causing the given depredation was applied. The spatial and temporal scales of their study were the wolf territory and 5 years. This meant that to be considered as a recurrence, the next depredation should occur within the same wolf territory as the initial depredation, and after a maximum of 5 years.

[96]: Bradley et al. (2015), 'Effects of Wolf Removal on Livestock Depredation Recurrence and Wolf Recovery in Montana, Idaho, and Wyoming'

[96] found that it took on average 115 days, 170 days and 730 days before the next depredation for groups *a*, *b* and *c* respectively. The difference between group *a* with no removal, and groups *b* and *c* was significant. However, the difference between group *a* and *b* was substantial only if the partial removal was applied in the first 7 days after the depredation. If not, the difference became marginal or even non significant after 14 days.

[96] also analysed these results at the spatial scale of the wolf pack, meaning that the next depredation is considered only if it was caused by the same pack as the first depredation, and not only in the same territory. They found '*a 7% increase in the probability of a recurrent event within 5 years for each animal left in the pack*.' Contrary to [97], neither sex nor the age influenced the depredation recurrence. They also found no specific influence of the removal of breeding females.

The third study [52] adopted a methodology comparable to [96] for a dataset from Michigan (USA) spanning over a period of 17 years. As previously, they compared the number of days before the next depredation, but here between 2 groups only: *a)* depredations for which no removal was applied before the next depredation if any, and *b)* depredations for which lethal removal was applied. The spatial and temporal scales of their study also differed from [96]: to be considered as a recurrence, the next depredation should occur before the end of the year of the initial depredation, and within the same cell. They tested three cell sizes: 2.56 km^2, 92.16 km^2 and 829.44 km^2.

[52]: Santiago-Avila et al. (2018), 'Killing Wolves to Prevent Predation on Livestock May Protect One Farm but Harm Neighbors'

[52] found that the probability of a recurrent event within a cell of 2.56 km^2 was higher in group *a* (with 168 depredations not followed by lethal removals), than group *b* (with 31 depredations followed by lethal removals). When expanding the spatial scale to 92.16 km^2, they found the opposite, with a probability of a recurrent event lower in group *a* ($n = 99$) than in group *b* ($n = 26$). At the largest scale of 829.44 km^2, they found results similar to the smallest scale, with a higher probability of recurrent event for group *a* than group *b*. However, none of their results were significant.

The *inter-site* comparison studies

Results from [97], [96] and [52] must be taken with caution. Besides the very unbalanced group sizes, the groups have not been controlled for the density of livestock or of wolves. These two variables represented high risks for confounding factors.

Intra-site comparison. This second approach consists in comparing the situation before and after the implementation of lethal removal within the same site. The control group is a group before the lethal measures, and the treated group is the same group but after the lethal measures.

This approach is also simply called the *before-after* study design [246]. This design intends to reduce the risks for confounding factors. Indeed, the risks to observe differences which are not due to the removal effect, but for example to the density of wolves or of flocks, are generally higher across space (when you compare two different groups of pasture) than across time (when you compare the situations at the same pasture before and after the removals). However, there are still risks of confounding factors. The depredation levels can change over time because of changes of environmental or pastoral factors. In this case, the depredation changes induced by removals would be confounded with the changes induced by the other factors [133].

[246]: Khorozyan (2021), 'Defining Practical and Robust Study Designs for Interventions Targeted at Terrestrial Mammalian Predators'

To date, only [99] used the intra-site comparison approach. They compared the number of depredations due to wolves in 7 pastures in Alberta (Canada) between *a)* the 4-year period when no lethal measures were applied and *b)* the 2-year period when trapping was implemented. They identified that depredations did not decreased after the 1st year of trapping, but did so after the 2nd year of trapping. This was due to a large drop in the abundance of wolves from 40 to 3 individuals in the 2nd year of trapping, because of the lethal removals and of poaching.

[99]: Bjorge et al. (1985), 'Evaluation of Wolf Control to Reduce Cattle Predation in Alberta'

The *intra-site* comparison study

It is difficult to conclude on the effect of lethal removals with the results of [99] as the size of the sample was very limited and above all, the implementation of lethal measures drove the studied wolf population to an almost extinction.

Correlation. This last approach is the farthest approach from the experimental design. This approach consists in establishing a mathematical link between depredation levels and lethal removals. Correlation is the simplest design to apply, and generally does not necessarily require as much information as the two previous approaches. This is probably why it was to date the most used approach to study the effect of lethal removals of wolves on depredation. However, correlation analysis does not allow the disentanglement of the cause and of the effect. For example, if there is a positive link between depredations and removals, you cannot confirm that it was the number of removals which increased the number of depredation and not the opposite.

To date, there are 5 studies relying on correlations only. The first three studies, [100, 140, 141], used the same dataset of depredations of the Northern Rocky Mountains (Montana, Idaho, Wyoming, USA) spanning over 26 years. The conclusions of the three studies were however different, basically because the first two studies used maladjusted models of correlation that the third study attempted to correct.

[100] assessed the relationship between the annual number of killed livestock on one side (total = 5 670), and the annual numbers of livestock, of wolves, of wolf breeding pairs and of wolves removed by lethal measures (total = 1 907), on the other side, through a correlation (more precisely a *generalised linear model*). To correct for the problem of directionality in the cause-effect relationship, they used a one-year time-lag. The number of killed livestock was from a given year, when the associated values of the factors or *explanatory variables* (number of livestock, of wolves killed etc...) were from the previous year. Main conclusions from [100] for the three states, combined or not, were that the lethal removals were efficient to reduce the level of depredations the next year only if wolf mortality exceeded 25%, otherwise lethal removals increased the level of depredations.

[100]: Wielgus et al. (2014), 'Effects of Wolf Mortality on Livestock Depredations'

But [141] noticed that almost all the data used by [100] had an increasing trend over time. With the time-lag, [100] had only corrected for the time sequence between variables, but not for the varying temporal trend inherent to each variable. Therefore, [141] explicitly included in the correlation analysis the effect of time on each variable. They also added, in addition to the lagged explanatory variables, the non-lagged version of these variables. Indeed, the number of depredated livestock in a given year could depend on the number of livestock of the previous year, but it could also depend on the number of livestock the given year. Main conclusions from [141] were that the lethal removals were efficient to reduce the level of depredations the next year regardless of wolf mortality.

[141]: Poudyal et al. (2016), 'Wolf Lethal Control and Livestock Depredations'

However, including more and more variables in a correlation analysis leads to a risk of *multicollinearity*[1], which can generate misleading results. [140] noticed that it was preferable to stay focused on the two variables of interest, the number of killed livestock and the number of killed wolves, and to exclude the other variables from the analysis. [140] also provided a better method to adjust for the temporal trends of the variables, which were not linear but sigmoidal. [140] concluded that the lethal removals reduced the number of depredation, but that this negative effect was only seen in the last years of the study period. They interpreted that this result was most likely due to the expansion of the wolf population in the first years of the study period. Thus, they concluded that the growth in the depredation levels in the early period was probably explained by the growth of the wolf population itself and not by the use of lethal removals.

1: The phenomenon when explanatory variables are linearly intercorrelated [247].

[140]: Kompaniyets et al. (2017), 'Modeling the Relationship between Wolf Control and Cattle Depredation'

The fourth study to rely on correlation design is the study of [98] which focused on Montana over a 11-year period (Figure 3.2). They assessed the relationship between the annual density of depredation events on one side, and the annual densities of wolves killed by targeted removals or public harvest on the other side, along other explanatory variables as livestock, wolf or pack densities. They treated the data on a finer spatial scale than the three previous studies, at the scale of 162 hunting districts (on average 1 280 km^2 for a district). To deal with the problem of directionality in the cause-effect relationship, they used the same technique as in [100] of one-year time-lag. Therefore, they did not exactly follow the design from [140]. However, they checked for multicollinearity risks and explicitly included an effect of the year on the variables in the correlation model[2]. [98] found that the public harvest density had a significant negative effect on the depredation density, but very weak, estimated at a reduction of ~ 6 depredation events for an annual harvest of 23% of wolves per district. The targeted removals were significantly related to an absence of depredation in a district, but had no significant effect on the depredation counts.

[98]: DeCesare et al. (2018), 'Wolf-Livestock Conflict and the Effects of Wolf Management'

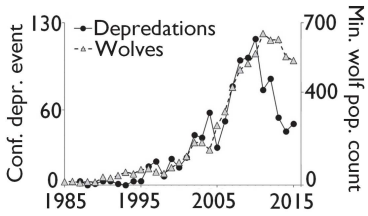


Figure 3.2: Annual numbers of confirmed livestock depredations by wolves (dots) and minimum wolf counts (triangles) in Montana, USA. The study of [98] only used data from 2004 to 2015. Credits: Adapted from DeCesare *et al.*, 2018 [98]

2: Year is included as a random intercept

The fifth and last correlational study is the only one relying on European data. It is the study of [67] which focused on the region of Asturias in Spain over a 8-year period. They assessed the relationship between the annual number of depredation events on one side ($\overline{x} = 2951$, $sd = 478$), and the annual number of wolves legally killed on the other side ($\overline{x} = 15$, $sd = 7$), along other explanatory variables as livestock, wolf pack or harvested ungulate numbers. As [98], they also treated the data on a finer spatial scale than the three first correlational studies, at the scale

[67]: Fernández-Gil et al. (2016), 'Conflict Misleads Large Carnivore Management and Conservation'

of 7 wolf management zones of roughly 1 100 km^2 each. To deal with the problem of directionality in the cause-effect relationship, they used the same technique as in [100] of one-year time-lag, but also used the number of wolves killed the same year as the depredations. To deal with the problem of varying trends over time, they used a similar approach to [141] by explicitly using year as an explanatory variable. This problem was however less risky here as variables were mostly constant over the study period compared to the American studies. Nonetheless, [67] did not mention they checked for multicollinearity risks. They found that the more wolves culled during the current or previous year, the more depredations. Contrary to [140], they concluded that culling is the cause for this increase. They also made the hypothesis that this could potentially result from pack dissolution itself responsible for an increase in the number of packs in the region.

The correlational studies

Correlational studies [67, 98, 100, 140, 141] involved large scales of analysis without controlling for confounding factors. They could not provide reliable interpretation on the cause-and-effect directionality of the relationship between depredation and removal. This limit adds to the difficulties to apply models that are appropriate to the data and to correctly evaluate the model quality.

What about France?

To date, no scientific study using French data has been published in a scientific journal. We are only aware of one unpublished scientific study[3], that was therefore not peer-reviewed: the study of [248] which used data for all France over the period 2008–2011. The approach used is the *intra-site* comparison. She compared the number of depredations due to wolves before and after the first day of validity of derogation decrees[4]. For the studied period, the number of legally removed wolves corresponded to 4 wolves only. So **the study analysed the effects of the deployments of humans to protect flocks rather than effects of removals**. I will nonetheless describe her results because they could be compared to our results on the effects of removals, and because her methodology, which has not been used in any of the previously mentioned studies, were interesting for developing our own methods.

3: I did not include the correlational study of [201] in the Regional Natural Park of Queyras because of the absence of methodological and result description concerning her analysis on culling.

[248]: Le Cam (2012), *Evaluation de l'efficacité de la mise en place de tirs de défense ou de prélèvement sur les attaques des troupeaux domestiques par le loup Canis lupus*

4: 195 defence culling, 15 harvest

[248] used discrete periods of time before each decree (from January or 30 days before the decree's date), and five periods after the decree (of 7, 14, 30 or 60 days after the decree, or up to the end of the year). She also used several discrete spatial scales. To be considered as related to the decree, a depredation should occur within the pasture(s) protected by the decree, or within a buffering circle of 2, 4, 6, 8 or 10 km radius around this pasture, or within the same massif.

To correct for the variations in the number of depredations across time that were not linked to the decrees[5], she used two strategies. First, she restricted her analysis to the decrees of August, and over a maximum period of 30 days before and after the decrees, when pastures were all mostly used by grazing flocks. She found that there is no significant change of the number of depredations before and after the decrees at all temporal and spatial scales with two exceptions. The depredations significantly decreased within a 2 or a 4 km radius buffers around the pastures protected by the decrees, when she compared a period of 7 days before and after the decrees. The depredations also decreased within the 2-km radius buffer when the period was extended to 14 days before and after the decrees.

5: *i.e.* to correct for confounding factors

In the second strategy, she used the ratio of the number of depredations over the total number of depredations of the massif. She found two possible results according to the temporal and spatial scales. The depredation ratio could not significantly change after the decree's dates, or the ratio could significantly decrease. The decrease was significant at the pasture only 30 days after the decrees, whether the comparison is done with a a period of 30 days before the decrees or with the period spanning from January of the same year. This decrease induced by the decrees was also significant at the other spatial scales, but the larger the buffer, the weaker the effect.

In the third strategy, she estimated the 'natural' annual dynamic of depredations by using the period of wolf colonisation of 1994–2011. She averaged the annual proportion of depredations over 15-day periods for this period. She then corrected the number of observed depredations with this estimated natural dynamic. She found that the depredations significantly decreased at almost all spatial scales, including the massif scale, and for almost all periods after the decree's dates. Consistently with the second strategy, she also found that the larger the analysed spatial scale, the weaker the decrease.

What about other Canids?

It could be interesting to extend the scope of our literature review to other species of predators. However, as developed in Chapter 1, the grey wolf has a particular social structure which complicates the study of the effect of its lethal control. Its high sociality makes it difficult to compare it to solitary predators. Nevertheless, two species of Canids close to the grey wolf have been controlled in order to reduce their depredations. These two species present a life in social groups too: the dingo (*Canis dingo*) in Australia [249] (Figure 3.3), and the coyote (*Canis latrans*) in North America (Figure 3.4).

[124] compiled 3 studies on the effects of lethal control of dingo: [138, 250, 251]. However, they all used approximations regarding both dingo's control and dingo's depredation. The three studies used the presence [138] or the number of distributed baits [250, 251], but had no record of the dead dingoes. They used the number of lactation failures as a proxy for calves lost to predation [138], or the total livestock production (number of produced calves [251] or sheep [250]). Therefore, their results are difficult to compare with the previously mentioned published studies on wolves. I will however highlight that [138] used an **experimental approach**, where he randomly assigned treatments of baiting, controlled for the environmental and farming variables and checked for dingo abundances. Its results were contrasted (43% where baiting increased lactation failures, 43% with no effect of baiting and 14% where baiting decreased lactation failures) likely because the number of sites was limited to 2 farms, each one with a baited and non-baited areas, with the experiment repeated over 4 and 3 years (*i.e.* therefore a total of 7 site-years). The two other studies used a **correlational design** with the issues inherent to this approach (see previous section about correlational studies).

[249]: Wallach et al. (2017), 'Cattle Mortality on a Predator-Friendly Station in Central Australia'

[124]: van Eeden et al. (2018), 'Carnivore Conservation Needs Evidence-Based Livestock Protection'



Figure 3.3: A cow, her calf (*Bos taurus*) and a dingo (*Canis dingo*) in Australia. Credits: Gerrit Schuirmann, in [249]

[138]: Allen (2014), 'Wild Dog Control Impacts on Calf Wastage in Extensive Beef Cattle Enterprises'

[250]: Allen et al. (2001), 'The Effect of Dingo Control on Sheep and Beef Cattle in Queensland'

[251]: Allen (2015), 'More Buck for Less Bang: Reconciling Competing Wildlife Management Interests in Agricultural Food Webs'

[124] also compiled 3 studies on the effects of lethal control of coyotes: [252–254]. They had a better level of information than the previous studies on dingos, because they knew the count of grazing sheep, the count of sheep killed by coyotes, and the removed coyotes, on a monthly or seasonal basis. [252] and [254] both focused on an agricultural research facility in California. [252] used a **correlational approach**, where the number of killed coyotes was lagged with different periods compared to the proportion of depredated sheep over the grazing sheep (*i.e.* kill rate). Most tested correlations provided borderline a significant or non-significant negative relations between both variables, but of low intensity. The study of [254] used an **intra-site comparison approach**. They tested the differences in sheep kill rates within a coyote territory between two periods of 3 months preceding and succeeding the selective kill of one of the breeding depredating coyote of the territory. They found sheep kill rates significantly decreased for 17 killed coyotes over 20. Finally, the last study [253] used an **inter-site comparison approach**. They compared the number of depredated sheep for 21 pairs of pastures located in Utah or in Idaho. Within a pair, there was one treated pasture (mean area of 45 km^2) and one untreated pasture of similar habitat and flock (mean area of 31 km^2). The treatment consisted in using an winter aerial coyote hunting. However, in both the treated and untreated pastures, ground control of coyotes was still used. Winter aerial hunting was not made for scientific purpose, which prevented the study to be experimental. They found the number of depredations in summers was significantly lower in treated pastures than in untreated pastures.



Figure 3.4: A sheep and two coyotes (*Canis latrans*) in California. Credits: Guy Connolly, in [127]

[252]: Conner et al. (1998), 'Effect of Coyote Removal on Sheep Depredation in Northern California'
[253]: Wagner et al. (1999), 'Effect of Preventive Coyote Hunting on Sheep Losses to Coyote Predation'
[254]: Blejwas et al. (2002), 'The Effectiveness of Selective Removal of Breeding Coyotes in Reducing Sheep Predation'

The identified gaps

Following this literature review on the studies about the effects of lethal removals of Canids on their depredations, I identified four gaps:

- **The majority of the published studies focused on the situation in North America**, especially in the contiguous USA. There is only one study about grey wolves in Europe [67] and three studies on dingoes in Australia [138, 250, 251].
- There were 8 studies which used a **correlational approach** over the 15 identified published studies. However, this approach, appearing simple at first sight, involves methodological choices that can be tricky, and does not allow for identifying with certainty the direction of the causal relationship[6].
- Among the risk for confounding factors, the identified studies using a comparison approach had **not all corrected for livestock presence or abundance** (*e.g.* [97]). This variable is the primary factor structuring depredation risk and should be considered.
- **Most studies analysed the effects of removals on discrete spatial and temporal scales**. They analysed the effect on a unique spatial scale[7] or with multiple categories of spatial scales (*e.g.* [52, 97, 248]). Concerning time, these studies compared fixed periods before and after the removals (*e.g.* [99, 248, 254], or they compared two pastures over fixed periods (*e.g.*[253]). Correlational studies used a monthly (*e.g.* [252]) or a year basis (*e.g.* [67, 98, 140]). Only studies analysing depredation recurrence used a continuous temporal scale, but combined it with discrete spatial scales ([52, 96, 97]).

6: As mentioned by [140], p.10, '*if one desires not only to predict the response* [i.e. *predict depredation according to removal levels], but also interpret the estimated model parameters, then much care must be taken so as not to put too much weight on these interpretations*'

7: *e.g.* predator territory [96, 254], pasture [99, 138, 253], hunting district [98], management zone [67], state [140]

3.3 Databases

Culling

We used the data compiled by the French administrations, the *Regional Department for the Environment, Development and Housing of the Region Auvergne-Rhône-Alpes* (DREAL AURA) and Office Français de la Biodiversité (OFB). This database listed at the national scale all the legal culling of wolves, but also all the detected poaching of wolves, from 2011 to 2020. All wolf bodies culled or found in the wild have to be examined by a veterinarian who performs autopsy (Figure 3.5). The authorisation of legal culling was given by decrees taken by the prefects of departments. The decrees were nominative and concerned one farmer or one group of farmers. Decrees for three classes of legal culling can be currently delivered [122] (Table 3.1). More details can be found in section *Application of lethal measures in France* in Introduction.



Figure 3.5: Autopsy of a wolf. The autopsy was performed by the veterinarian Dominique Gauthier, assisted by two agents of OFB, Yannick Léonard (right) and Thierry Coulée (left), in the departmental veterinary laboratory of Gap, Hautes-Alpes, France. Credits: O. Grente

Table 3.1: The three types of culling in 2021 in France [122].

	Simple defence culling	**Reinforced defence culling**	**Harvest**
Conditions	Implemented non-lethal protective measures	Implemented non-lethal protective measures. ≥ 3 depredations for the last 12 months.	An *'exceptional'* level of damages on several flocks protected by non-lethal measures and simple defence culling
Validity	≤ 5 years	Ongoing year	Ongoing year
Application	Only one shooter, near the flock. The shooter can be the recipient of the decree or any person mandated by this recipient.	Operations of generally several days supervised by *brigadiers* or by *lieutenants de louveterie*. ≤ 10 shooters, near flocks.	Operations supervised by *brigadiers* or by *lieutenants* in a specific area. Or during a big game hunting. Limits in the number of wolves that can be culled.
Time	Any moment	During an operation	From July to December

Be aware that these classes and conditions of their applications can have slightly changed through time. For example, the harvesting class was before separated in two classes as the defence culling classes. The *lieutenants de louveterie* have also been progressively equipped with thermal cameras in the last few years only. The number of *brigadiers* have grown with the recruitment of several agents in the last few years.

We used the 91% of the database on culling fulfilling these conditions:

- The culling was geolocated,
- The culling was dated,
- The culling was legal, therefore it was not poaching.

We focused on culling that occurred in the Alpine range or close, covering the whole regions Provence-Alpes-Côtes-d'Azur (PACA) and AURA (at the exception of the departments Ain, Loire and Rhône where there was no culling). We defined this **study area** for two reasons. First, no information on the pastoral surfaces outside the regions of PACA and AURA was available. Second, wolves culled outside this study area were

mainly lone wolves which dispersed far and whose territory was very isolated. Their deaths could only lead to an absence of attacks up to the next settlement. This context was totally different from the one in the Alpine range where the wolf population was dense and replacement in vacant territories was quick.

Each culling event corresponded to only one culled wolf. If two wolves were culled simultaneously, they counted as two culling events. For each culling event, we had:

- The date and location,
- The class of culling,
- The type of shooter (farmer, *brigadier*, *lieutenant*, hunter),
- The sex, the age class (pup, subadult or adult) and the reproductive status of the culled wolf if the body has been found[8].

8: The reproductive status of the year can only be evaluated for females, by observing the presence of placental marks.

The analysis encompassed...

- **362** culling events, where one wolf had been culled,
- from **2011** to **2020** inclusive,
- in PACA and AURA (except Ain, Loire and Rhône).

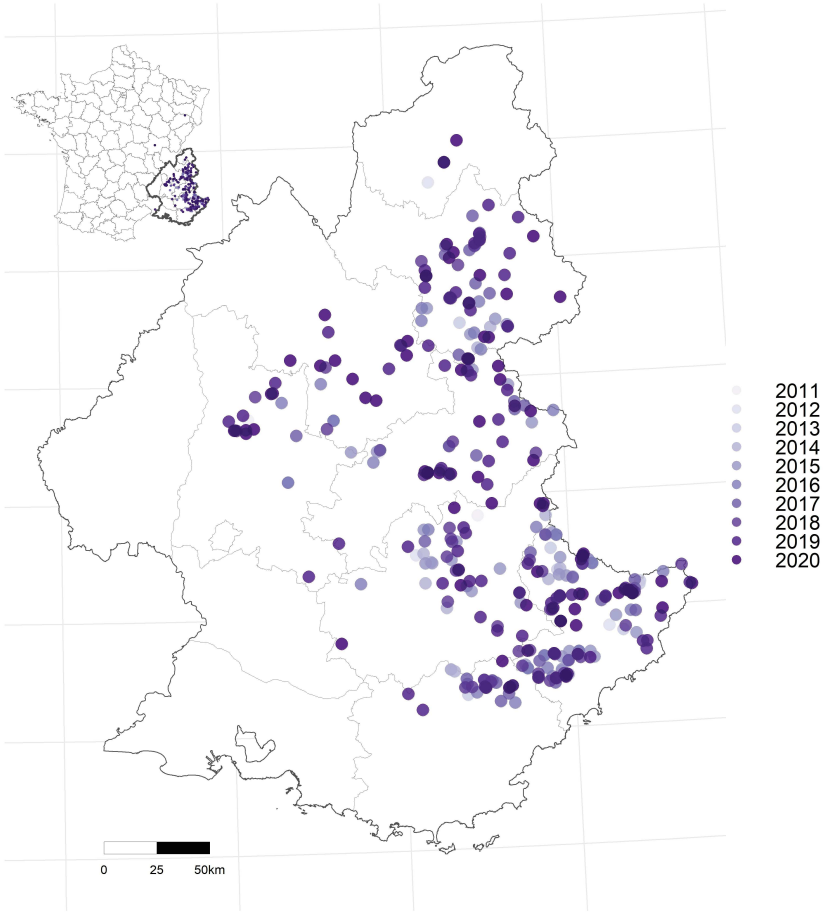


Figure 3.6: Map of the 362 culling events of wolves from 2011 to 2020 in the study area, that were used in the analysis. The inset shows the culling events without restriction to the study area. Credits: O. Grente

Depredations

We used the data from the database *Géoloup* of the French administration DREAL AURA. This database listed all the claims of depredation on livestock that were suspected to be caused by wolves in France. Each claim was checked in the field by an accredited governmental agent who used a standardized protocol [115]. Up to 2019, the Ministry of Ecology compensated for any killed farmed animal for which wolf responsibility could not be discarded, regardless of protective measures. Therefore, most if not all depredations were reported if noticed.

We used the 87% of *Géoloup* fulfilling these conditions:

- The responsibility of wolves were not excluded,
- The depredation was geolocated within the study area,
- The depredation was dated,
- The depredation concerned at least one killed sheep[9]

The analysis encompassed...

- **28 651** events of depredation of wolves on sheep,
- from **1994** to **2020** inclusive,
- restricted to PACA and AURA (except Ain, Loire and Rhône).



Figure 3.7: Consumption of a sheep by a wolf in Hautes-Alpes, France. Credits: Réseau Loup-Lynx.

[115]: Duchamp et al. (2012), 'A Dual Frame Survey to Assess Time– and Space–Related Changes of the Colonizing Wolf Population in France'

9: We restricted the analyses to depredations on sheep only, as they constituted 90% of depredations on livestock in France.

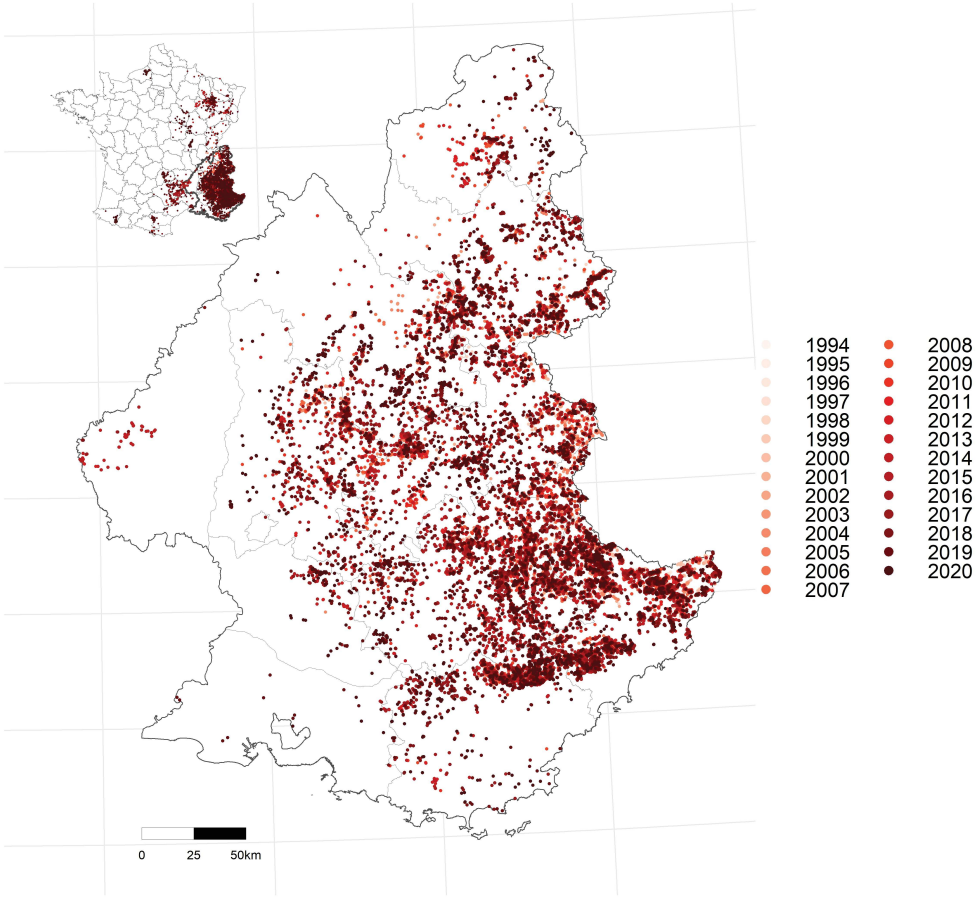


Figure 3.8: Map of the 28 651 depredations on sheep from 1994 to 2020 in the study area, displayed from the youngest to the oldest, that were used for the analysis. The inset shows the depredations without restriction to the study area. Credits: O. Grente

Pastoral surfaces

We used the data from the second pastoral census of *Institut national de recherche en sciences et technologies pour l'environnement et l'agriculture* (IRSTEA), made during the period 2012-2014. This census only concerned the regions AURA and PACA and indexed all the pastoral units at high altitude used by flocks during summer, and the other pastoral zones at lower altitudes, used by flocks in summer or during other seasons. However, the pastoral zones which were not exclusively used by flocks (*e.g.* also used for growing crops) were not indexed in the census. More information about this census is available in Chapter 4.

We grouped the pastoral units and zones in the same file, and called them **pastoral surfaces**. Pastoral surfaces were very useful in our analysis because they delimited the spatio-temporal area where depredation events could have occurred. Therefore, our analysis was restricted to the pastoral area from this census.



Figure 3.9: Flock of sheep guarded by a shepherd and her livestock protection dogs, in July 2021 in Hautes-Alpes, France. Credits: M. Jégu

We used the 40% of the pastoral census fulfilling these conditions:

- The pastoral surface in use (not abandoned),
- The pastoral surface used by sheep,
- The period of use of the pastoral surface was available,
- The pastoral surface was in the study area.

However, the period of use of the pastoral surface was not given the same way for the pastoral units and the pastoral zones. For pastoral units, the exact months in use were available. For pastoral zones, only the season in use was available. To remedy this situation, we attributed to the pastoral zones the months corresponding to the seasons for which they were used (spring: March to May, summer: June to August, fall: September to November, winter: December to February).

For each pastoral surface, we had at our disposal the following information:

- Its geolocation and precise limits,
- The pastoral type: unit or zone,
- The unique ID of the pastoral surface,
- The size of the sheep flock using the surface,
- The months in use by flocks.

The analysis encompassed...

- **4 987** pastoral surfaces,
- restricted to the study area.,
- covering 1.9 km^2 on average (sd = 3.0),
- covering 9541 km^2 in total (15.3% of the study area).

The pastoral data used in the analysis is displayed over the study area in Figure 3.10. Maps of the size of sheep flocks and the grazing duration in days of these pastoral surfaces are available in Figure 4.2, or online at https://oksanagrente.shinyapps.io/Hotspots-SuppFig1/.

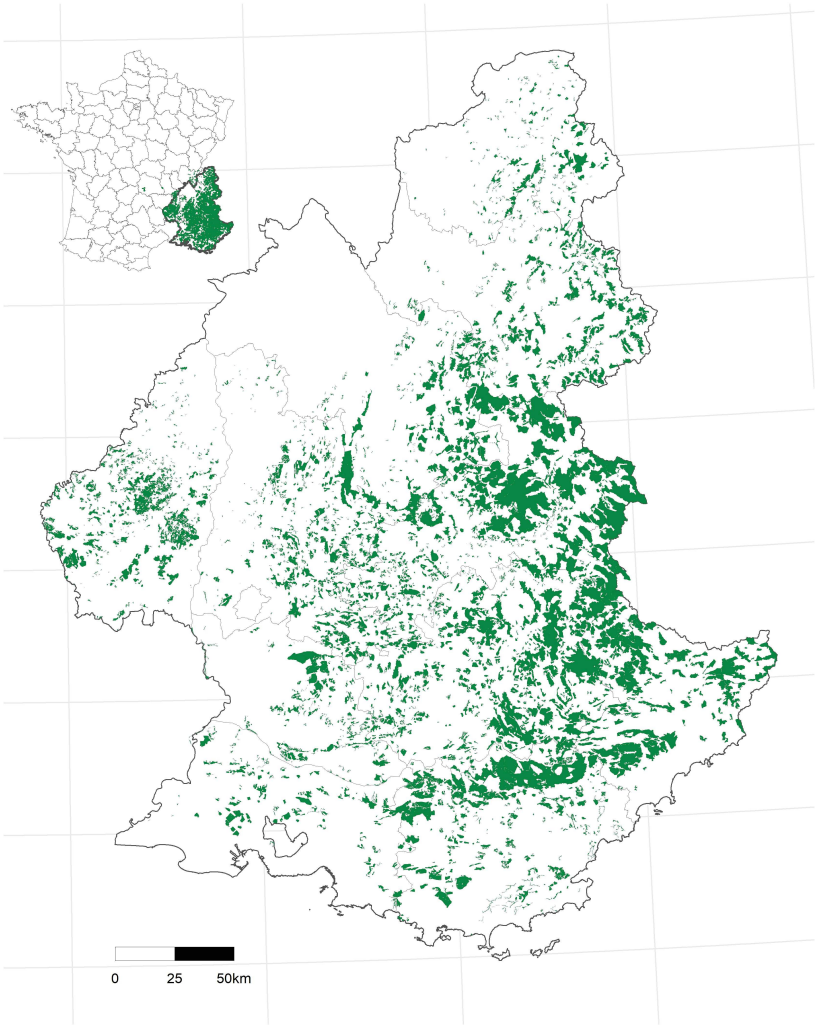


Figure 3.10: Map of the 4 987 pastoral surfaces with grazing sheep from the second census made by IRSTEA in 2012-2014, over the study area. The inset shows the pastoral surfaces without restriction to the study area. Credits: O. Grente

Consistency between the databases of depredations and of pastoral surfaces

We needed to make sure that both the depredation data and the pastoral data were consistent, whether it was in space or in time. However, some inconsistencies between both sources of data could exist. Some depredation events were outside pastoral surfaces, or occurred at a month

for which the pastoral surface was not supposed to be in use according to the pastoral census.

These mismatches could result from several reasons:

- Errors were made during the input process of the depredation events in the *Géoloup* database,
- Depredation events occurred in pastoral surfaces which were not part of the pastoral census of IRSTEA,
- A change in the spatial or temporal use of the pastoral surfaces has occurred since the census.

We dealt with these mismatches with two main corrections: 1) **the spatial relocation of depredation events close enough to pastoral surfaces** and 2) **the addition of the month of the depredation event to the list of the months in use of the pastoral surface**.

Figure 3.11 relates precisely the approach we used for each depredation event to solve the spatial and temporal inconsistencies. A decision was made for each event. The decision depended on the consistency between the event's location and month, and the spatial and temporal information of the closest pastoral surfaces to this event.

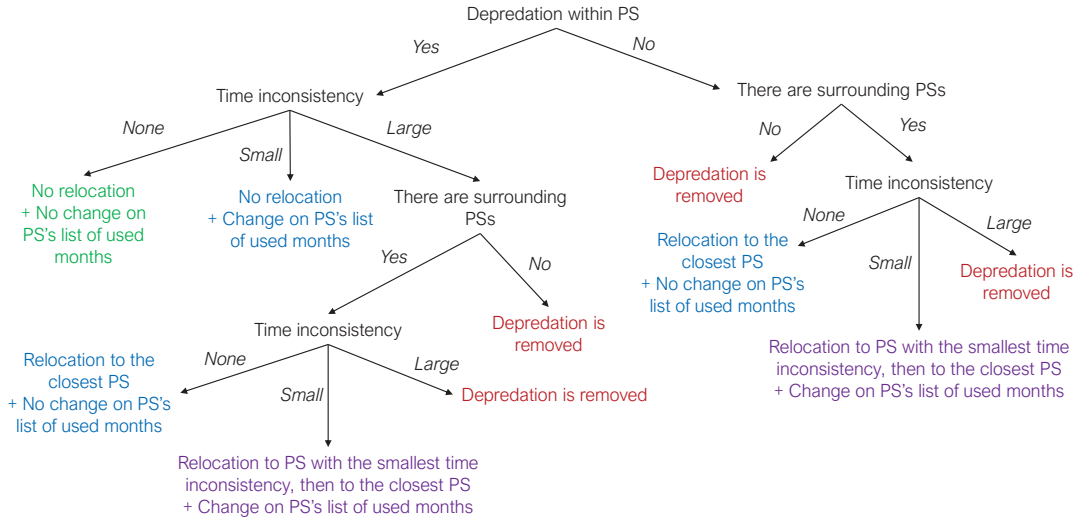


Figure 3.11: The process used to deal with the inconsistencies between the depredation and pastoral data that were used in the analysis. PS means Pastoral Surface. The process is applied for each depredation event, one by one. Credits: O. Grente

These were the four types of outcomes which could result from this process for each depredation:

- No relocated without change on PS. There was no inconsistency between the depredation and pastoral data. The group of depredation events in green corresponded to the events where no change was applied: they were not relocated, and no modification on the months in use of their pastoral surfaces was made.
- No relocated with change on PS. The group of depredation events in blue corresponded to the events where only one change was made. In this group, only the list of the months in use of the pastoral surface within which the event was located was changed, through the addition of the event's month to this list. It could only happen if the time inconsistency between the depredation event and its

pastoral surface was not too large. Thus, it was a way to deal with the minor changes in the temporal use of the pastoral surfaces.

- Relocated without change on PS. The group of depredation events in blue corresponded to the events where only one change was made. In this group, only the location of the event was changed. The event was relocated in a close pastoral surface. This relocation could result for two reasons. First, because the time inconsistency between the depredation event and its pastoral surface was too large, and the event needed to be relocated to a pastoral surface which had no time inconsistency with the event. Second, because the event was outside any pastoral surface but still close enough to some surfaces for which there was no inconsistency in time. Thus, it was a way to deal with the errors in the input process of the depredation events.
- Relocated with change on PS. The group of depredation events in purple corresponded to the events where two changes were made. This could result from two situations. First, because the time inconsistency between the depredation event and its pastoral surface was too large, and the event could only be relocated to a pastoral surface with a small time inconsistency. Second, because the event was outside any pastoral surface but still close enough to some surfaces for which the inconsistency in time with the event was not too large. Thus, it was a way to deal with both the minor changes in the temporal use of the pastoral surfaces and the errors in the input process of the depredation events.
- No relocatable. The group of depredation events in red corresponded to the events which were too far from any pastoral surface to be relocated. Thus, it was a way to deal with both the errors in the input process of the depredation events and the depredation events occurring in pastoral surfaces which were not part of the pastoral census of IRSTEA.

This approach implied two arbitrary factors: what was considered as *events outside pastoral surfaces but still close to pastoral surfaces*, and what was considered as a *small inconsistency in time* between the event's month and the months in use of the closest pastoral surfaces.

We chose to consider a distance of **500 m** for relocation ('*There are surroundings PSs*' in Figure 3.11), and to define to **3 months** the maximum gap in time considered as a small gap in time and for which the month can be added to the pastoral surface database ('*Time inconsistency*' in Figure 3.11).

The results of the process to deal with inconsistencies between depredation and pastoral data are presented in Table 3.2.

A total of 2 778 depredation events (10%) were put aside from the analysis due to a too large inconsistency with the pastoral data. The impacts of these arbitrary thresholds on the relocation process, and thus on the general analysis, should be evaluated through a sensibility analysis.

Contrary to the depredations, the culling events did not require to be located within pastoral surfaces, as a wolf could be wounded by a shoot in a pastoral surface, but found dead or culled outside the pastoral surface. Moreover, the harvest type of culling did not necessarily occur within pastoral surfaces (see section *Culling*).

Result	Count	Proportion
No relocated without change on PS	17357	61
No relocated with change on PS	2934	10
Relocated without change on PS	5166	18
Relocated with change on PS	416	1
No relocatable	2778	10
Total	28651	100

Table 3.2: Results of the process used to deal with the inconsistencies between the depredation and pastoral data that were used in the analysis. PS means Pastoral Surface.

Operations of *brigadiers*

We used the data compiled by the OFB. This database listed all the reports of operations realised by *brigadiers* in France. The reports included the location and hours of the operation, some environmental and pastoral parameters of the operation, regardless of the result of the operation. These operations were mainly from the reinforced defence culling type (see section *Culling*).

We used the 64% of the database which corresponded to the geolocated and dated operations that took place in the study area. Generally, an operation of brigadiers took place over several consecutive nights (or 'intervention') on the same area or pasture. A report was made for each intervention. We grouped the interventions that belonged to the same operation, in other words interventions which were located in the same area and of close dates. We decided to set the maximal distance between the locations of two interventions of the same operation at **2 km**, and to set the maximal time gap between two interventions of the same operation at **2 days**. As previously, the impacts of these arbitrary thresholds should be evaluated through a sensibility analysis.

For each operation, we had at our disposal the following information:

- The beginning date and ending date of the operation,
- The centroid of the operation,
- The number of interventions,
- The shooting class of the operation (see section *Culling*),
- The total duration in hours of the operation,
- The number of shooters on average per intervention,
- The mean distance of the shooting groups to the flock during the interventions of the operation,
- The presence of livestock guarding dogs or fences during the operation,
- The final result of the operation (wolf culled or not) and the total number of culled wolves if any

The analysis encompassed...

- **145** operations of *brigadiers*,
- from **2016** to **2020** inclusive,
- located in the study area restricted to PACA and AURA (except Ain, Loire and Rhône).



Figure 3.12: Preparation of an operation of livestock protection by *brigadiers* of OFB in France with the shepherds of a flock. Credits: B. Muffat-Joly

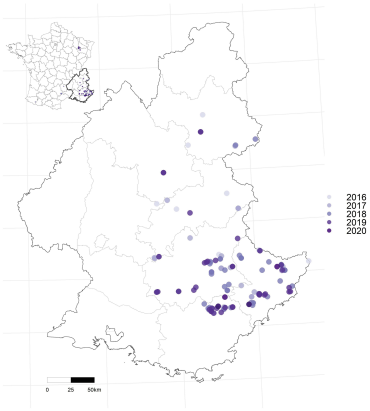


Figure 3.13: Map of the 145 *brigadiers*' operations from 2016 to 2020 in the study area, that were used in the analysis. The inset shows the operations of *brigadiers* without restriction to the study area. Credits: O. Grente

3.4 Analysis

We developed a methodology that was adapted to respond to the challenges raised by our available data, but also by filling the gaps of the previous studies on the subject that were mentioned earlier in section *The identified gaps*.

1. **To minimise the risk of confounding effects.**

In our analysis, data were part of administrative registers. Their collection had not followed the protocol of an experimental study. The study of these kind of data, already collected, is called 'retrospective study'.

Among the possible approaches for retrospective studies, we chose the *before-after* study design (*i.e.* the *intra-site* comparison). We therefore compared the spatio-temporal distributions of the depredations before and after the culling events.

We could have applied the other design of retrospective studies, the *inter-site* comparison. We would have compared the spatio-temporal distributions of depredations in sites with culling and in sites without culling. However, this design involved a higher risk for confounding effects. Indeed, the differences between the depredation distributions in two different pastures could be due to the differences linked to the pastoral practices or the environmental conditions between these pastures, and not to the difference in the culling application. Therefore, it would have been more difficult with this design to conclude about the effect of culling.

The risk for confounding factors was however not absent in the *before-after* design. The pastoral or environmental conditions could evolve through time Therefore, there was a risk to attribute to the culling a change in the depredation distribution that was actually due to an evolution of the pastoral or environmental conditions of the pastures before and after the culling events. For example, it was plausible that, in response to a high level of depredation, a farmer intensified the non-lethal protective measures in addition to culling. It would therefore be impossible to disentangle the effects of the non-lethal and lethal protective measures. The non-lethal protective measures would be here a confounding effect. However, we expected that the differences through time within the same pasture are lower than those between pastures. In short, we expected a lower risk for confounding effects with the *before-after* study design (*i.e.* the *intra-site* comparison) than with the *inter-site* comparison.

2. **To distinguish between the culling effects and the seasonal dynamic of depredations.**

Amongst the potential confounding effects of our analysis, the one linked to the seasonal dynamic of depredation was the most preoccupying one. Indeed, depredations were subject to large seasonal variations. The most prevalent seasonal variation was related to the pastoral practices, because flocks were grazing only during a limited part of the year, and removed from pastures when the climate cooled. The depredation distributions was conditional on the presence of sheep.Thus, the progressive decrease in the presence of sheep grazing in the Alpine range from autumn had to be dissociated from the potential effect of culling events.

3. **To analyse the culling effects at the appropriate spatial and temporal scales.**

The last major technical challenge our study concerned the spatial and temporal scales of analysis. The culling effect could be noticeable at one specific spatio-temporal scale, but not at another. As we have seen previously, most studies focused on one or several fixed scales. This required to multiply the analysed scales in order to decrease the risks to miss the scale where the effects of culling apply. To avoid this problem, we opted for an analysis of the culling effects along a continuous spatial and temporal gradient around the culling events.

We based our methodology on:

1. The comparison of the spatio-temporal distributions of depredations, before and after the culling events,
2. through the use of a spatio-temporal buffer and...
3. the kernel method.

The spatio-temporal buffer

We attributed to each culling event a **spatio-temporal buffer**. The spatio-temporal buffer can be visualised as a cylinder which was centred on the culling event (Figure 3.14).

The diameter of the cylinder corresponded to the spatial scale: it was a 2D circle centred on the culling event (in purple in Figure 3.14), which had the role to scan the pastoral space around the culling.

The height of the cylinder corresponded to the temporal scale: the part above the culling scanned the time before the culling, and the part below the culling scanned the time after the culling.

The set of depredations falling into this spatio-temporal buffer was considered as '*related to*' the given culling event, and were thereafter

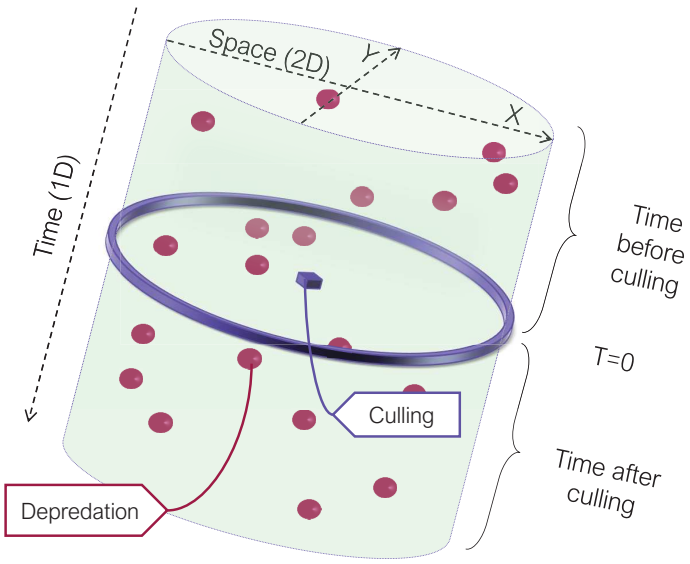


Figure 3.14: Diagram of the 3D spatio-temporal buffer, which was computed for each culling event. Credits: O. Grente

selected for the analysis. It was easy, by modifying the diameter or the height of the buffer, to test different gradients of spatial and temporal scales to evaluate the culling effect.

I will now present how we constructed these buffers and the challenges they raised.

Spatio-temporal limits

We decided to limit **the diameter of the buffer at 20 km**, meaning that the depredation events falling into a radius of 10 km around a culling event were considered as spatially related to the given culling.

We wanted to approximate the wolf territory radius, estimated at 7–8 km in France through telemetry and genetic tracking [115]. This way, the reports of depredation within the wolf territory could be observed in the analysis results. We could have chosen a larger radius, first because the centre of the pack territory overlapping the culling, if any, was not expected to be exactly at the culling location, and second because the report of depredation could have been outside the pack territory. However, when we tried higher radiuses, the depredation distribution was compressed towards the smallest values of spatial distances, and therefore the results were difficult to read. This is why we focused on the 10 km radius.

[115]: Duchamp et al. (2012), 'A Dual Frame Survey to Assess Time– and Space–Related Changes of the Colonizing Wolf Population in France'

We decided to limit **the height of the buffer at 180 days**, meaning that the depredation events occuring 90 days before and 90 days after the culling were considered as temporally related to the given culling.

We chose this temporal limit in order to analyse the effect of culling on one full season if the culling occurred in the middle of the season, or on two successive seasons if not. We could also have increased this limit. As previously, when we did so, the depredation distribution was compressed around the culling date, as most of flocks were not grazing three months before or after culling (meaning depredations were unlikely to occur at high levels outside the grazing period).

The effects of culling were analysed..

- within a radius of **10 km** around each culling event,
- over a period of **90 days before** and **90 days after** each culling event.

Limit date of the analysis

It was necessary to ensure that the buffers did not overlap the period for which there was no available data on depredation events. In other words, we could not analysed the culling events of which the temporal buffer overlapped with 2021, as we only had available depredation events until 2020 inclusive. With an analysis covering 90 days after the culling events, we should restrict the analysis to culling events occurring before the **3rd October 2020**.

Because of this constraint, we lost from the analysis 15 culling events, of which the dates were close to the end of 2020, and of which the buffers

overlapped with year 2021. Thus, **we had left 347 culling events to analyse** at this part of the methods.

The effects of culling were analysed..

- with culling events occurring before the **3rd October 2020**,
- because the available depredation dataset stopped to 2020.

Limit space of the analysis

As said previously, the analysed depredation events could only occurred within pastoral surfaces. This meant that the spatial buffer of each culling event was in fact composed by pastoral area and empty non-pastoral space. This pastoral area was constituted by all pastoral surfaces within the 10 km radius circle around the culling event.

However, it could happen that some pastoral surfaces partially overlapped with this circle, meaning that some parts of the pastures were outside the circle. We could have truncated such pastoral surfaces, keeping only the parts inside the circle. However, this would have been problematic for the next part of the analysis. In section *Depredation seasonality*, the simulation of the seasonal dynamic of depredations was at the pastoral level. Because we had no idea which specific part of the pastoral surface a flock was grazing in at a given time, the pastoral surfaces could therefore not be divided, and should be considered as indivisible units.

Therefore, the circle of a buffer (represented by the purple ring in Figure 3.14) could actually be extended over 10 km, to include the outside parts of the pastoral surfaces overlapping the 10 km circle (Figure 3.15). This meant that the depredations located outside the 10 km radius circle but within the pastoral surfaces overlapping this circle were considered as part of the buffer. However, the pastoral surfaces which were not overlapping the 10 km radius circle, but were within the extended circle, were not considered as part of the buffer.

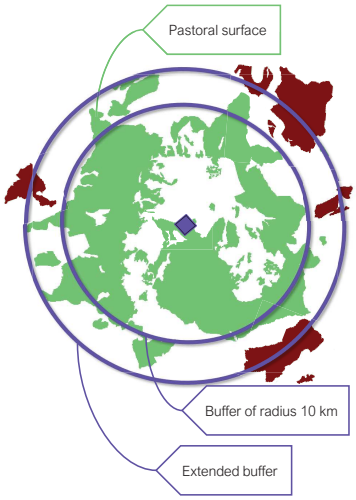


Figure 3.15: Schematic representation of an extended buffer around a culling event (purple dot). Pastoral surfaces which are partially or totally overlapping with the buffer of radius of 10 km are in green. Pastoral surfaces which are not are in red. Note that a pastoral surface could be a multipolygon (several green areas not connected to each other). The limits between pastoral surfaces are not shown. Credits: O. Grente

The spatial buffer could be extended...

- over 10 km from the culling event,
- in order to include the whole area of the pastoral surfaces overlapping with the spatial buffer
- because we could not cut the pastoral surfaces.

Interactions between buffers

Two buffers could overlap both in space and time (Figure 3.16). This raised a challenge because the effect of a culling could potentially be impacted by the effect of another one. Therefore, if we included them as such, we would not study the effect of a unique culling event. We needed to separate the analysis of the unique culling events and the analysis of the interacting culling events. The analysis of interacting culling events will be presented in section *The interacting culling events*. I will pursue

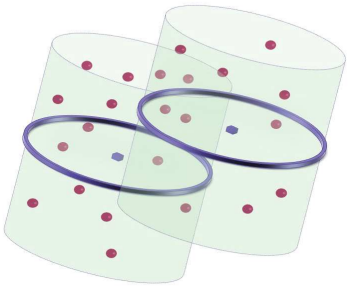


Figure 3.16: Diagram of two overlapping buffers of culling events, both in space and time. Credits: O. Grente

here with the unique culling events for now. So I needed to identify these unique culling events.

The number of pairs of culling events of which the buffers were overlapping was 462. We should not be surprised that the number of pairs of overlapping buffers exceeded the number of culling events that we analysed, here 347. Indeed, for 347 events, there could be a maximum of $347 \times \frac{(347-1)}{2} = 60031$ pairs. The 462 pairs of overlapping buffers concerned 80% of the set of buffers, with 277 culling events. Let's learn more about the spatial and temporal distances that separated the culling events of these 462 pairs, and how frequently these pairs were encounters per year (Figure 3.17).

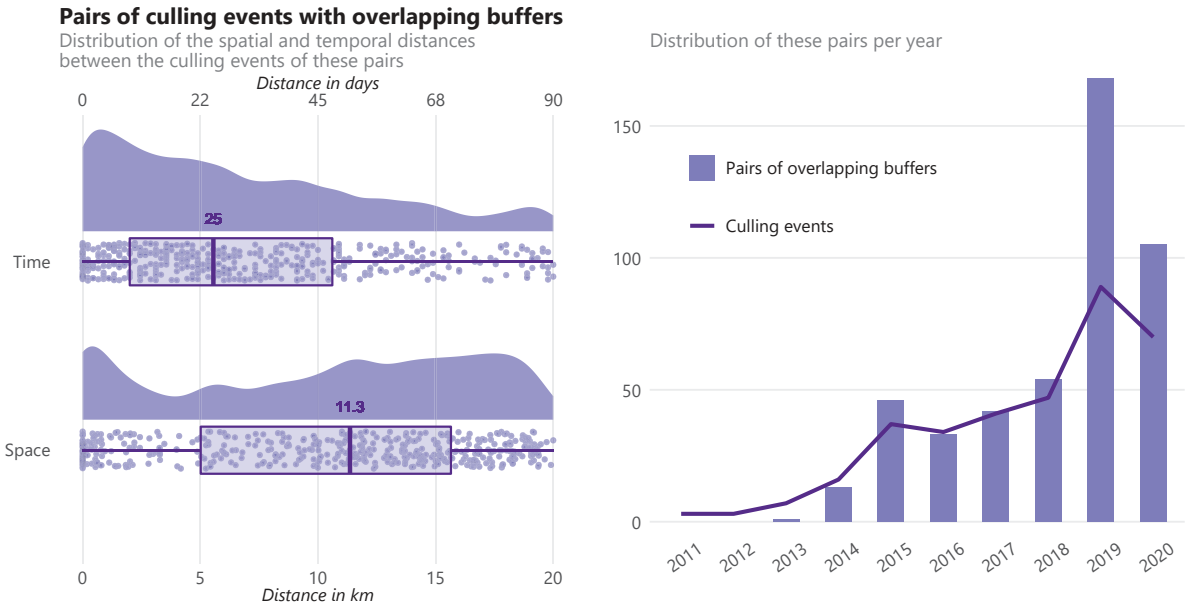


Figure 3.17: Information about the 462 pairs of culling events with overlapping buffers. Credits: O. Grente

Without surprise, the number of pairs of overlapping buffers increased through time as the number of culling events increased[10] (Figure 3.17).

The distribution of the spatial distances between the culling events of these pairs was spread over the range 0–20 km (Figure 3.17). For 75% of the pairs, the culling events were separated by more than 5 km. Hence, from the 462 pairs of overlapping buffers, only 115 pairs were separated by less than 5 km, and they concerned 147 culling events. We noticed that among these 115 pairs, most of them were aggregating towards very low values of spatial overlapping, close to 0, suggesting a high spatial overlap of the two culling events of these pairs.

The distribution of the temporal distances between the culling events of these pairs was drawn towards lower values than the distribution of spatial distances (Figure 3.17). Half of the pairs was separated by at least 25 days. Hence, from the 462 pairs of overlapping buffers, 230 pairs were separated by less than 25 days, and they concerned 209 culling events.

The advantageous configuration would be pairs of culling events where the temporal distance was low, but with a high spatial distance, or the opposite. For such pairs, the level of interactions between both buffers could be judged as low. It would therefore be possible to reintegrate such

10: Do not forget that the number of events in 2020 was truncated in our analysis because we had to remove those of the end of the year, as explained in section *Limit date of the analysis*.

culling events into the analysis of the effects of unique culling events. However, this required to define what is a low distance, whether it was spatial or temporal.

To help us, let's look simultaneously to spatial and temporal distances for the 462 pairs of overlapping buffers (Figure 3.18). By chance, we observed that most of pairs for which the temporal distance was less than 25 days had spatial distances of at least 10 km. There was eventually only few culling events that were simultaneously close in space and time. Amongst these events, most of them fell into the red area encompassing temporal distances from 0 to 10 days, and spatial distances from 0 to 2 km in Figure 3.18. In total, there was 51 pairs of culling events, corresponding to 79 culling events, that fell into these conditions. If we widened to an area encompassing temporal distances from 0 to 25 days, and spatial distances from 0 to 5 km (the bottom left square in Figure 3.18), we encompassed 76 pairs of culling events, corresponding to 111 culling events.

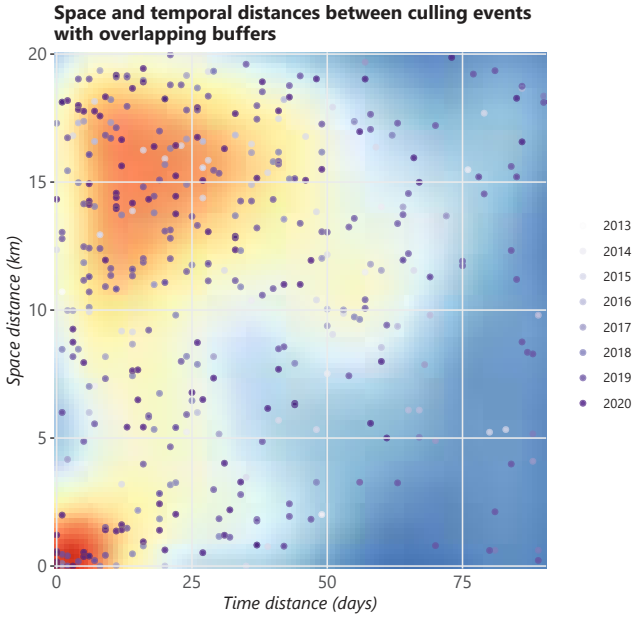


Figure 3.18: Spatial and temporal distances between the 462 pairs of culling events with overlapping buffer Credits: O. Grente

Given the previous results, we decided to define as low risks of interaction the pairs of overlapping buffers involving a spatial and temporal distances of more than **5 km** and **25 days** between the culling events[11]. We therefore excluded from the analysis of the effects of unique culling events, the 111 culling events concerned by pairs which were not considered as involving low risks of interaction. Thus, **we had left 236 culling events to analyse the effects of unique culling events**. The 111 culling events with high risks of interaction were kept aside for the analysis of the effects of interacting culling events (section *The interacting culling events*).

11: This was an arbitrary choice that would have required a sensitivity analysis. For more security, we could have extended this definition of low risks to higher spatial and temporal distances between culling events. However, we would have lost a considerable number of culling events considered as unique. This was a weakness of the analysis: it was hard to define the limit between interacting culling events.

The effects of unique culling were analysed..

- with **236 culling events**,
- which were separated from each other by at least **5 km**,
- and by a period of at least **25 days**.

Transition from 3D to 2D

The three-dimensional property of our data (space in 2D, time in 1D) greatly complicated the analysis. There was no available method to analyse the effects of the spatio-temporal distribution of one dataset of points, here the culling events, on the spatio-temporal distribution of an other dataset of points, here the depredation events, when considering both distributions in a 3D. In [255, 256], the provided methods required that the dataset of the culling events should have been only a spatial distribution. However, it was impossible to put aside the temporal component of the culling events in the analysis of their effects on the depredation level, even more when using a *before-after* design.

[255]: Diggle (2014), *Statistical Analysis of Spatial and Spatio-Temporal Point Patterns*
[256]: Wikle et al. (2019), *Spatio-Temporal Statistics with R*

We circumvented this problem by:

1. Translating the 2D space into a 1D space,
2. Making the information of the culling events implicit.

We adopted a 1D space. This meant that we transformed the set of coordinates (X,Y) for each depredation event to a unique value representing the spatial distance of the depredation event to the centre of the buffer, and therefore to the culling event. Thus, we ended up with depredation data in 2D, one dimension for space, one for time, which broaden the scope of possible methods.

Moreover, it allowed us to make the information of the culling events implicit. Indeed, there was no need for the next part of the analysis to know exactly where and when the culling event was, nor the depredation events. The relative spatial and temporal distances between the culling event and its related depredations were enough to study the culling effect on the spatio-temporal distribution of the depredations. Concrete explanations will come in section *Buffer finalisation*.

However, the simplification of the 3D depredation dataset into a 1D depredation dataset was not without consequences. To understand the challenge, let's focus on the 2D spatial dimension of the buffer. It was represented by a circle (the cylinder, which is in 3D, only appears when considering the time dimension). Imagine now a set of depredation events, randomly located within the circle. It would be likely to find more depredation events on the edges of the circle than close to its centre. Indeed, the further you are from the centre of the circle, the larger the periphery of the ring. This phenomenon is represented in Figure 3.19.

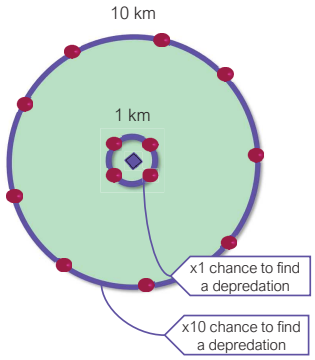


Figure 3.19: Diagram of randomly located depredation events (red dots) at 1 km or 10 km from a culling event (purple dot). Credits: O. Grente

In a 2D space, this phenomenon is not a problem. Each depredation event has a precise spatial location X,Y. There would be an equal chance to find a depredation at the location, let's say X_1, Y_1, very close to the center, than at the location X_{100}, Y_{100} at the edges of the circle.

In a 1D space however, this phenomenon is problematic because the spatial location is simplified to the spatial distance to the centre. To give you a concrete example, the extreme ring at 10 km from the culling event corresponds to a perimeter of 63 km, when the ring at 1 km from the culling event would only encompass 6 km. With a randomly located depredation dataset, you would have 10 times more chance to find a depredation over the 10 km ring than over the 1 km ring, just because the 10 km ring encompass 63 km and the 1 km ring only 6 km. This is not

due to the depredation 'biological' pattern, but only to methodological bias, due to the space simplification.

It was therefore necessary to apply a spatial correction to correct this bias of space simplification. Within a buffer, the farther the depredation event from the culling event, the more penalised this depredation would be, and the weaker its weight into the analysis. For example, one depredation found at 1 km from the culling should weight the same weight than a set of 10 depredations found at 10 km from the culling. The spatial correction applied to each depredation event should then be $1/r$, with r the spatial distance at which the depredation event was from the culling event Figure 3.20.

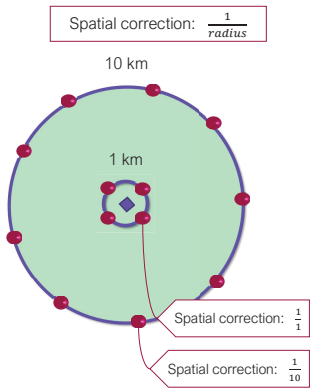


Figure 3.20: Diagram of the spatial correction required for the depredation events (red dots) found at 1 km and at 10 km from the culling event (purple dot). Credits: O. Grente

Unfortunately, the challenge did not end here. Remember that the space where depredations could occur was delimited in our analysis to the pastoral surfaces. The simple correction $1/r$ could therefore not be applied as such. Indeed, in some buffers, the pastoral surfaces could be aggregated at a medium distance from the culling event and almost non-existent at the farthest distances, as in Figure 3.21. In this situation, it was not at the largest radius where it was the most likely to find a depredation, because there was less pastoral space available. The depredations were most likely found at the radius encompassing the highest pastoral surface. The depredations found on this radius were those which must had the lowest weight in the analysis.

To take this problem into account, we sliced up the circle of each buffer into 200 rings of progressive radius, all centred on the culling event of the buffer. For example, two non-adjacent rings are shown in Figure 3.21. There was no empty space left between rings. The width of the rings were the same for all buffers, in order to make sure that the following spatial

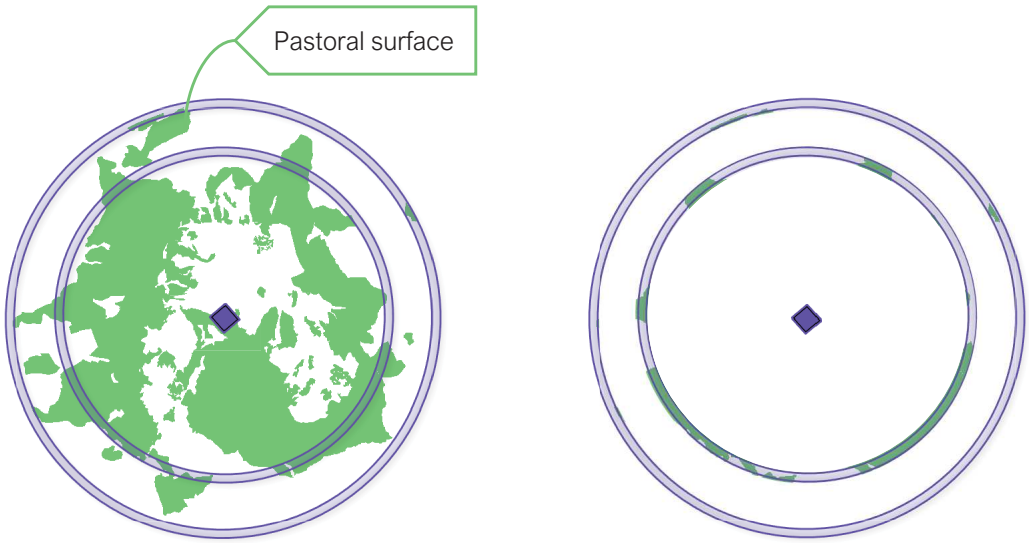


Figure 3.21: Map of the pastoral surfaces included in the extended spatial buffer around a culling event, and representation of two rings as applied in the spatial correction. The pastoral area of the two rings corresponded to the sum of the green area within each of these rings, as shown on the right side. The inside ring crossed more pastoral surfaces than the biggest ring, therefore having a larger pastoral area than the largest ring. The depredations events from the inside ring, if any, weighted individually less than those from the largest ring in the analysis, because of the spatial correction $1/pa$. NB: The limits between pastoral surfaces are not shown, as well as the pastoral surfaces which were are only overlapping the extended spatial buffer but not the circle of 10 km radius (see Figure 3.15). Credits: O. Grente

correction was applied similarly for all buffers. Because the circle could extend to more than 10 km because of overlapping pastoral surfaces, the last ring had not necessarily a radius of 10 km but it could be more. This meant that the width of the rings were defined according to the 200 adjacent rings required for the buffer with the largest extended circle (Figure 3.15). The largest extended buffer corresponded to 20.2 km.

The pastoral area pa contained into each ring of each buffer was then computed. Henceforth, the spatial correction attributed to each depredation event of each buffer became $1/pa$, where pa was the pastoral area corresponding to the ring on which the depredation event was located.

Methods of analyses of multiple 3D datasets are limited...

- so we opted for a simplification of the 2D space into a 1D space,
- which required to attribute a **spatial correction** to the depredation events,
- which was dependent on the spatial distribution of the pastoral surfaces.

Buffer finalisation

After selecting the 236 unique culling events which fulfilled the following conditions:

1. The temporal buffer of the culling event did not overlap year 2021 where depredation data was not available,
2. The culling event was separated from the other culling events by more than 5 km and 25 days.

For each culling event, we selected the depredation events contained within their spatio-temporal buffers, in other words, the depredations occurring 90 days before or 90 after the culling event, and located within the pastoral surfaces totally or partially contained within the 10 km radius circle around the culling event (Figure 3.22).

For each depredation event of each buffer, the following information was available:

- The spatial distance to the culling event (in km)
- The temporal distance to the culling event (in days)
- Its spatial correction $1/pa$

The final step was to compile in a single table all the depredation events (and their above information) contained in the 236 computed buffers around the unique culling events. **The total of depredation events analysed was 7 747.** It was possible that a depredation event was part of several buffers. In the table, this depredation event would appear as many times as the number of buffers it was in, each row containing the information of this depredation event relative to one buffer.

Thanks to the simplification of the 3D spatio-temporal information into 2D, it was possible to visualise the spatio-temporal distances between the 7 747 depredations events and their culling events in a single figure. For this, the culling events were all represented at the (0,0) location of the figure, where the *x-axis* represented the temporal distance of

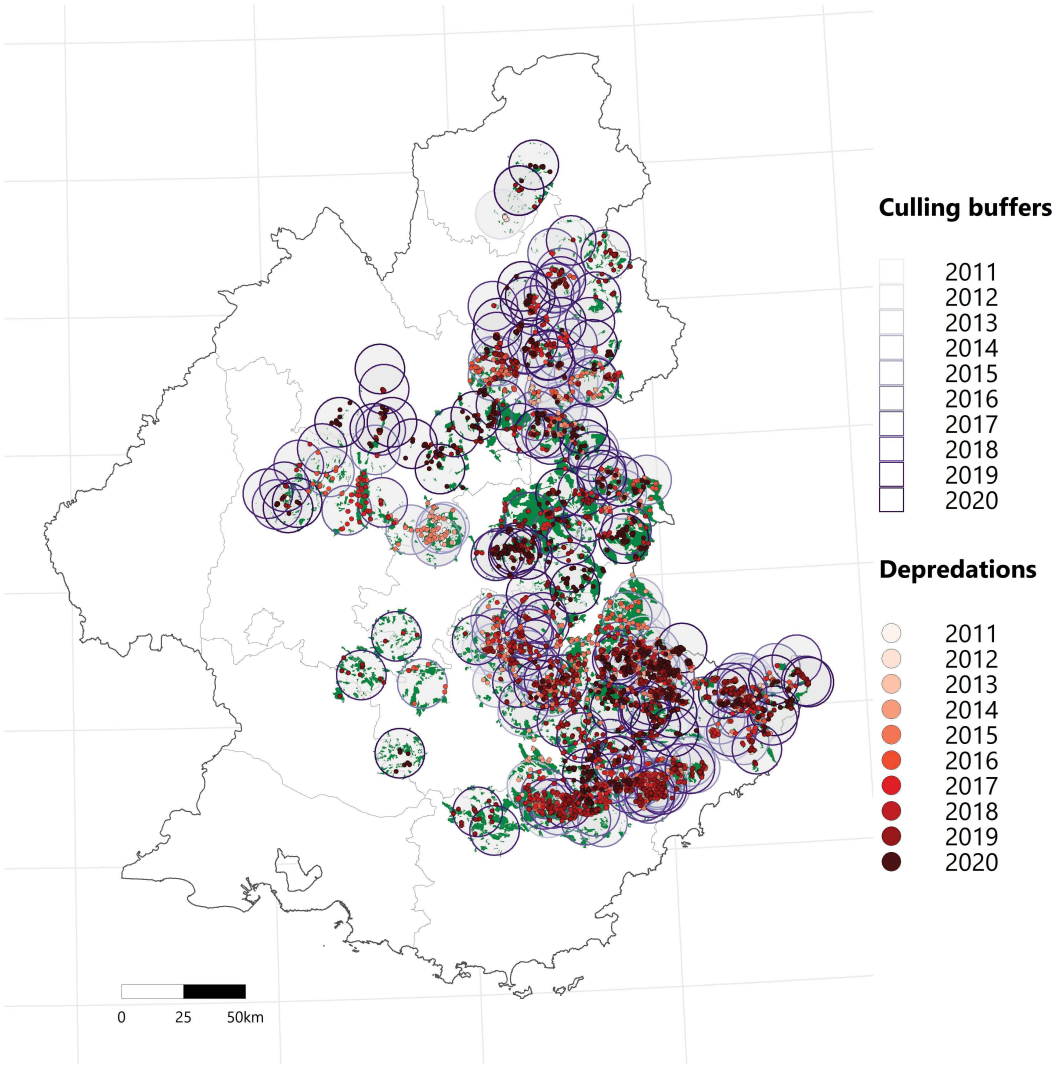


Figure 3.22: Map of the spatial buffers of 10 km radius of the 236 culling events of wolves in the study area, that were used in the analysis of the effect of unique culling. Pastoral surfaces integrally or partially overlapping these buffers are shown. The showed depredation events were those that were spatially and temporally part of the buffers. Credits: O. Grente

a depredation event to the culling event of its buffer, and the *y-axis* represented the spatial distance of a depredation event to the culling event of its buffer. The culling events were therefore implicit in the figures: only the depredations were actually represented. Thus, we worked within a 2D environment (1D for time, 1D for space), with a single type of dataset, namely the compiled depredation dataset of the 236 buffers.

This visualisation is given in Figure 3.23.a. Each point represented a depredation event. Its location in the figure was according to the time and spatial distances to the culling event of its buffer. The vertical dotted purple line represented the date of the culling event. All the depredations located at the left of this line were occurring before the culling event date (*i.e.* their time distance to the culling event was negative). The horizontal dotted purple line represented the location of the culling event. The further a depredation from this line, the further the depredation occurred from the culling event of its buffer.

Depredations occurring in the same buffer have the same color in Figure 3.23.a. It was quite hard to disentangle the different culling events. We

could extract some culling events to have a clue of the tendency of the culling effects for these events (Figure 3.23.b).

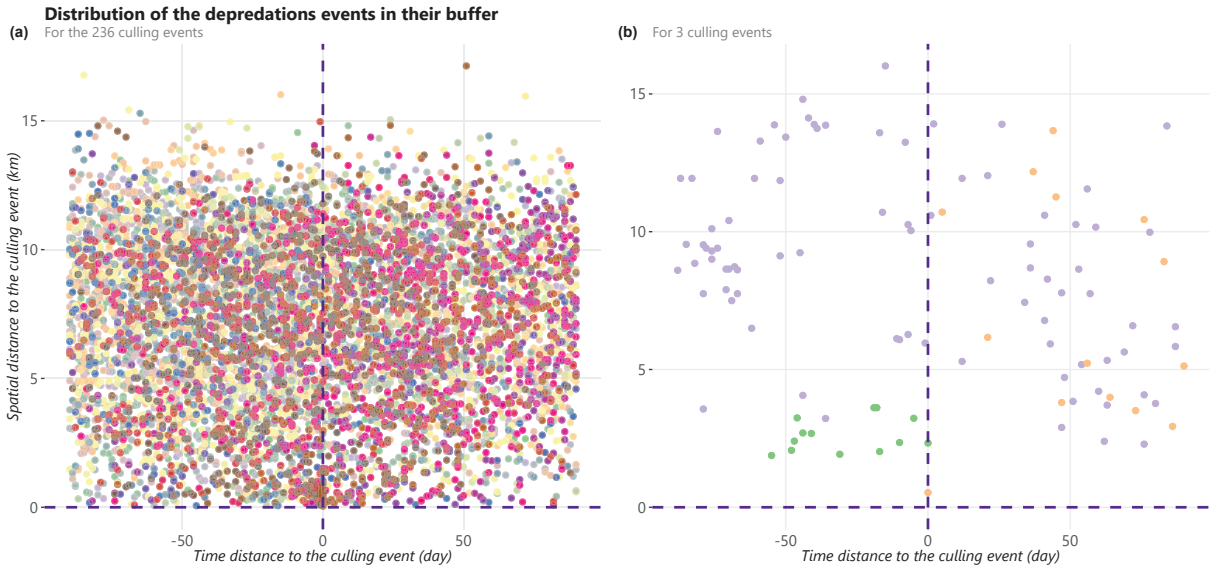


Figure 3.23: Distribution of the depredations events according to the time and spatial distances to the culling events of their buffer, for (a) the 7 747 depredation events of the buffers of the 236 unique culling events, and (b) the 111 depredations events for three of these culling events. Depredations occurring in the same buffer have the same color. The depredations occurred 90 days before or 90 days after their associated culling event. The depredations could occur above 10 km from their associated culling event, despite the 10 km radius chosen for the spatial buffer, because of they could be within the partially overlapping pastoral surfaces which were extending above the 10 km limit (see section *Limit space of the analysis*). Credits: O. Grente

However, we could not analyse the effect of culling by going through the 236 culling events one by one. We needed to use a statistical method to analyse from Figure 3.23.a the general tendency of the spatio-temporal distribution of depredations around the culling events.

The analysis of the 236 unique culling events...
encompassed a total of **7 747 depredation events**.

The kernel estimation

The depredation intensity

To analyse the general tendency of the spatio-temporal distribution of depredations around the culling events in Figure 3.23.a, we need to evaluate the **intensity** of this distribution. Traditionally, the intensity is defined as *the expected density of points per spatial unit* [257]. The intensity can be seen as a function of Cartesian coordinates, which would attribute to each couple of coordinates (X,Y), a value of intensity.

[257]: Baddeley et al. (2015), *Spatial Point Patterns: Methodology and Applications with R*

In our analysis, we reduced the buffer information from 3D to 2D (section *Transition from 3D to 2D*). In Figure 3.23.a, the *x-axis* and *y-axis* represented the temporal and spatial distance to the culling event, respectively. The aim of the analysis was then to estimate, for each couple of coordinates X,Y in Figure 3.23.a, the **depredation intensity**.

To visualise the method, you can imagine that Figure 3.23.a was divided into a large number pixels. Each pixel had a centre of coordinates X (time),

Y (space). The depredation intensity of each pixel needed to be evaluated. We chose to divide the spatio-temporal area into a large number of pixels, **40 000 pixels**, also called '*units*'.

The depredation intensity of each pixel was done through a **kernel estimation**.In technical terms, the method consisted in applying Gaussian kernels. Schematically, the method consisted in applying, over Figure 3.23.a, a 3D bell over each depredation event, the top of the bells being centred on the depredation events. The kernels were not restricted to the pixel of the depredation, but overlapped the adjacent pixels. When two or more kernels were found in the same pixel, they merged, creating a higher kernel that would have been found with only unique kernel. Therefore, the more aggregated depredations there were in a unit, or in a group of adjacent units, the more the kernels overlapped. Visually, this translated by peaks of intensity in Figure 3.23.a. Mathematically, the number of overlapping kernels on a specific unit was corresponded to the depredation density of the unit.

The kernels (or bells) could be more or less smoothed, *i.e.* overlapping more or less adjacent units (as if the bell was more or less melting, respectively). If the smoothing was too strong, we were not able to see the details in the spatio-temporal distribution of the depredation events because a lot of kernels overlapped. On the contrary, if the smoothing was not strong enough, the kernels would not have sufficiently overlapped, and the trends in the spatio-temporal distribution of the depredation events would have not emerged. Therefore, an appropriate smoothing parameter for the kernels to balance these two side-effects was required. After multiple tests, we chose the smoothing parameters of **2 days** for the temporal axis, and of **500 meters** for the space axis. All the kernels had the same smoothing parameters.

The kernel estimation took into account the spatial correction that we had previously defined in section *Transition from 3D to 2D*. Thus, if a depredation event had a low spatial correction, then its kernel would less contribute to the depredation density of a unit. This had the consequence to change the measure of the unit. Thus, the number of overlapping kernels on a specific unit was not corresponding any more to the depredation density of the unit, because all the depredations had not an equal weight: some could weight more than others. Therefore, the kernel estimation we used estimated the depredation density per unit, which was defined as:

Definition 4 *The density (or intensity) of a unit was the sum of the depredation spatial corrections (i.e. weights) of the depredations events of which the kernels overlapped this unit.*

We applied a constraint on the kernel estimation, in order to better distinguish between the *pre-culling* and the *post-culling* spatio-temporal distributions of the depredation, occurring before and after the culling events, respectively. This constraint consisted in creating a barrier between the depredation events occurring before and after the culling events, visually corresponding to the vertical purple dotted line in Figure 3.23. The kernels of the depredations occurring before the culling event (*i.e.* with $x < 0$) could not contribute to the density calculations of any unit located after the culling event (with $x > 0$), and *vice-versa*.

The analysis was done in R 4.0.2 [193]. We used the R packages *sf* [258], *sp* [259] and *fields* [260] to handle the spatial data, and *spatstat* [261] and the function *kde2d.weighted* from *ggtern* [262] for data analysis.

[193]: R Core Team (2020), *R: A Language and Environment for Statistical Computing*

[258]: Pebesma (2018), 'Simple Features for r: Standardized Support for Spatial Vector Data'

[259]: Bivand et al. (2013), *Applied Spatial Data Analysis with R*

[260]: Nychka et al. (2017), *Fields: Tools for Spatial Data*

[261]: Baddeley et al. (2005), 'Spatstat: An R Package for Analyzing Spatial Point Patterns'

[262]: Hamilton et al. (2018), 'Ggtern: Ternary Diagrams Using Ggplot2.'

Clues for interpretation

The culling events were not equally represented in the analysis. It was depending on two factors:

- The number of depredation events within their buffer,
- The sum of the spatial corrections of these depredations.

The higher these numbers were for a culling event, the more the culling event would be represented in the analysis. We can see in Figure 3.24 the distributions of the culling events according to these two parameters, and how some culling events stood out. This meant that some culling events were less represented in the analysis. This was therefore important to keep in mind for the result interpretation: **the general tendency could mask the effects of some culling events**.

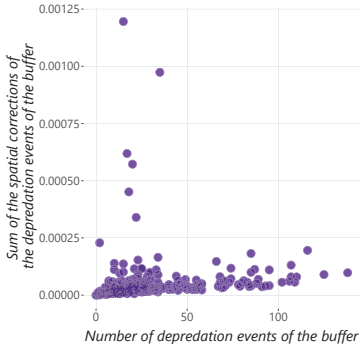


Figure 3.24: Sum of the spatial corrections of the depredation events contained within the buffer for each of the 236 unique culling events, according to the number of depredation events contained within the buffer. Credits: O. Grente

We decided not to compute a unique value summarising the depredation intensity level before the culling events, and after (*e.g.* sum of all the depredation intensities associated with a negative (or a positive) temporal distance in the kernel figure). We wanted to avoid an oversimplification of the results: it was necessary to keep the information of depredation intensities relative to their occurrence in space and time. I believe it was important that the results showed that no unique binary answer could be provided to the question of the efficiency of culling events: **the depredation process occurs on large spatial and temporal scales and, in my opinion, cannot be summarised into one unique value, whether it is statistical or only mathematical**.

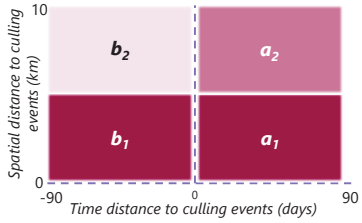
Consequently, the interpretation of the results was based on the kernel figures only. This allowed scientists but also managers to grasp in one single figure the tendency of depredations around the culling events, in space and time. I discuss this choice in more details in the discussion of this chapter or in section *Methods* in Chapter 5.

To determine if culling reduced the depredation intensity, we compared:

1. The intensity of depredations before and after the culling events at the same spatial distance.
2. The spatial spread or report of predations (Figure 3.25).

Definition 5 *A **spread of depredation in space** was suspected when depredation intensities remained equivalent between b_1 and a_1 (or were higher in a_1 than in b_1), and were higher on a_2 than in b_2. A **report of depredation in space** was suspected when depredation intensities were higher in b_1 than in a_1, but higher in a_2 than in b_2.*

(a) Case of spread



(b) Case of report

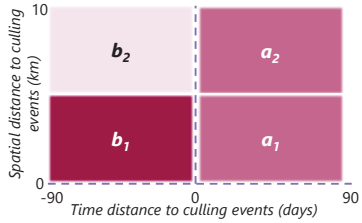


Figure 3.25: Schematic representations of a case of spread (a) and of report (b) of depredations in space. Credits: O. Grente.

The kernel estimation...

- analysed the intensity of the spatio-temporal distribution of depredations around the culling events,
- over 40 000 spatio-temporal units,
- with smoothing parameters of 2 days (*x-axis*) and 500 meters (*y-axis*),
- and was applied separately for the depredations occurring before and after the culling events.

All the eggs in one basket

Once we applied the kernel estimation to the 7 747 depredation events selected for the 236 unique culling events, we obtained the results presented in Figure 3.26. What we saw was that the depredation density of a few units was so high compared to the rest of the units, that it was flattening the results, *i.e.* the visible density values above zero were only located at a few units.

These high depredation density values were called '*outliers*'. They were extreme values compared to the rest of the distribution. In our case, the outliers made the distribution of the depredation intensity 'right-skewed' (Figure 3.27): almost all depredation values were constrained towards low values, except a few outliers. The highest encountered value was 0.020.

There is not a single possible threshold above which values are defined as outliers, but generally, the following threshold is used: $Q_3 \pm 1.5 \times (Q_3 - Q_1)$, where Q_1 and Q_3 are the 1st and 3rd quantiles of the distributions (meaning that 25% and 75% respectively of the values are less than Q_1 and Q_3). In our case, the outliers systematically were above the 3rd quantile. Therefore, we could define the outliers in our case as:

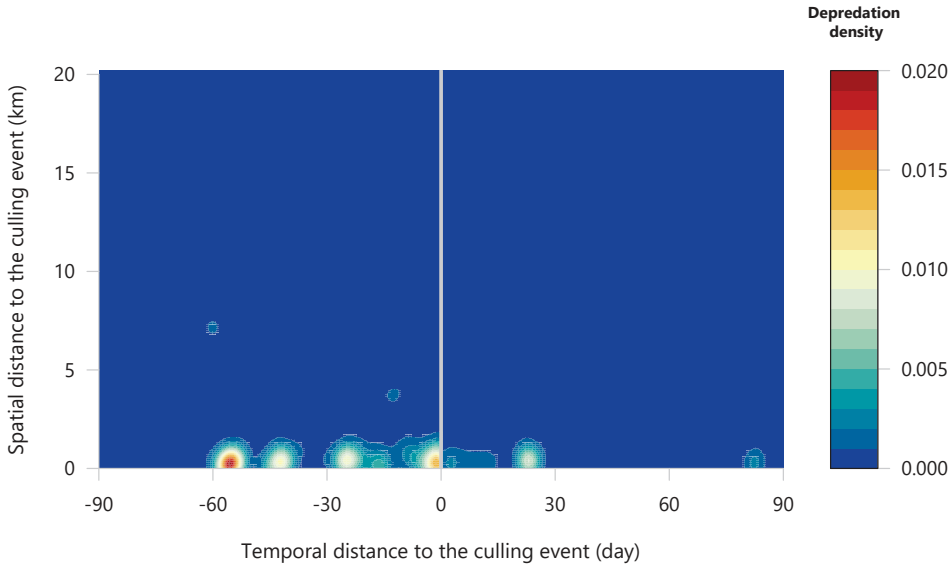


Figure 3.26: Estimation of the depredation density per unit of time and space around the 236 unique culling events. The depredation density of a unit was defined in Definition 4. Credits: O. Grente

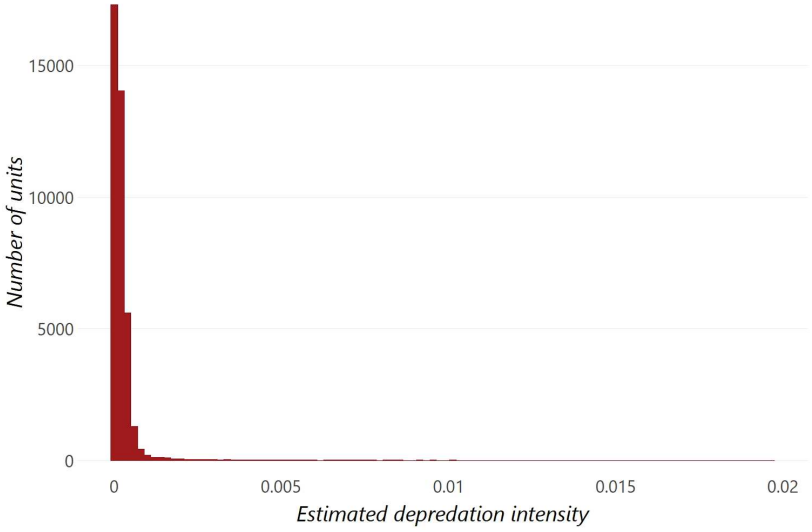


Figure 3.27: Distribution of the estimated depredation density values of the 40 000 units of time and space compiled for the 236 unique culling events. Credits: O. Grente

Definition 6 *The threshold above which a depredation density value of a unit was considered as an outlier in our study was defined as:*

$$Q_3 + 1.5 \times (Q_3 - Q_1) \tag{3.1}$$

where Q_1 and Q_3 are the 1st and 3rd quantiles of the depredation density distribution (meaning that 25% and 75% respectively of the values are less than Q_1 and Q_3).

We investigated the origins of these outliers. Even if the depredation density of these areas was high, it was very unlikely that the depredation density was close to zero everywhere else, especially when knowing that most of culling events were occurring in depredation hotspots (Figure 3.22, Chapter 4). These values could be partly due to specific depredations with very large spatial corrections, especially because these depredations were very close to the culling event of their buffers (therefore in circles where pastoral area was small, see section *Transition from 3D to 2D*)[12].

12: Note that the same phenomenon of outliers also appeared when using the simple spatial correction $1/r$

A correction to smooth the influence of these outliers was therefore required. To this end, **we set the highest depredation value of a unit at the outlier threshold** (Equation 6). This meant that all the depredation density values of units exceeding this threshold were equalling this value after the correction was applied (hereafter, the *outlier correction*).

Let's see the results in Figure 3.28. The distribution of the depredation events around the unique culling events showed a heterogeneous intensity across time and space. The depredation density was high essentially high near the culling event locations (*i.e.* near the value 0 of the *y-axis*), before or after the culling events. The high density values were found up to 60 days before the culling events. After the culling events, the high density values could be found up to 85 days, but not with as much continuity as before the culling events. Thus, between 30 days and 80 days after the culling events, the depredation density was low, at the exception of two short peaks of density in time around 32 days and 58 days after the culling events. At greater spatial distances from the culling event, high density values were mostly found before the culling events, generally up

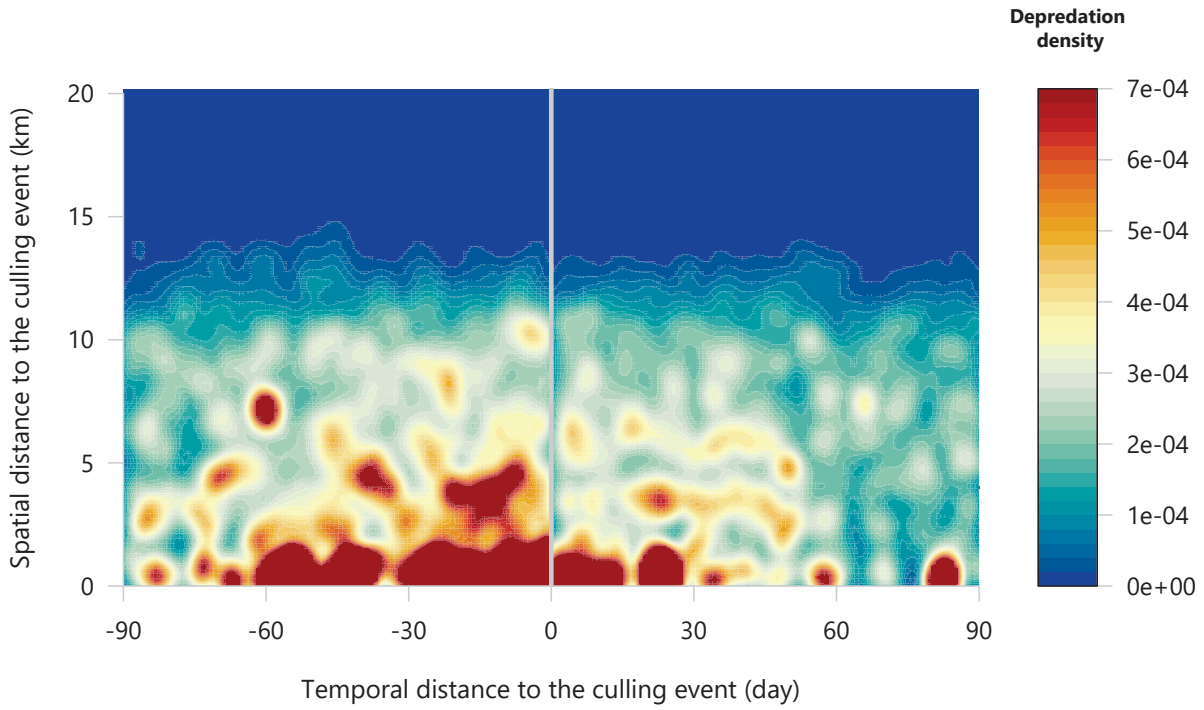


Figure 3.28: Estimation of the depredation density per unit of time and space around the 236 unique culling events. The depredation density of a unit was defined in Definition 4. The highest density values were brought to the outlier threshold. The depredations involved in the analysis were found inside the pastures partially or integrally overlapping the circle of 10 km radius around the culling events. Depredations were therefore scarcer above 10 km from the culling events, as the pastures were generally not spread out over large distances outside the circle of 10 km radius. Credits: O. Grente

to 5 km around the culling events, except for a peak at around 7 km at -60 days. The results did not show depredation spread or report around the culling events, in the limits of 10 km around the culling events.

However, a question remained unanswered: **are we observing the effect of unique culling events, or the effect of depredation seasonal dynamic, especially due to the pastoral dynamic?** Indeed, in Figure 3.28, there was no time correction applied to the analysis, only spatial correction. This meant that the analysis did not correct for the fact that flocks could have left the pastures at some point before or after the culling events. Therefore, the low density parts of the results, especially 30 days after the culling events, could be a reflect of a lower flock density rather than a culling effect. Let's correct for this bias in the next section.

The first results of the effects of unique culling events...

- showed that depredation intensity was high before and after the culling events,
- but was found over a larger continuous time period before the culling events,
- however this could reflect pastoral dynamic more than the culling effect.

Depredation seasonality

Data exploration

Let's visualise and compare in Figure 3.29 the seasonality of the pastoral grazing, of the depredations and of the culling events that were previously analysed in Figure 3.28.

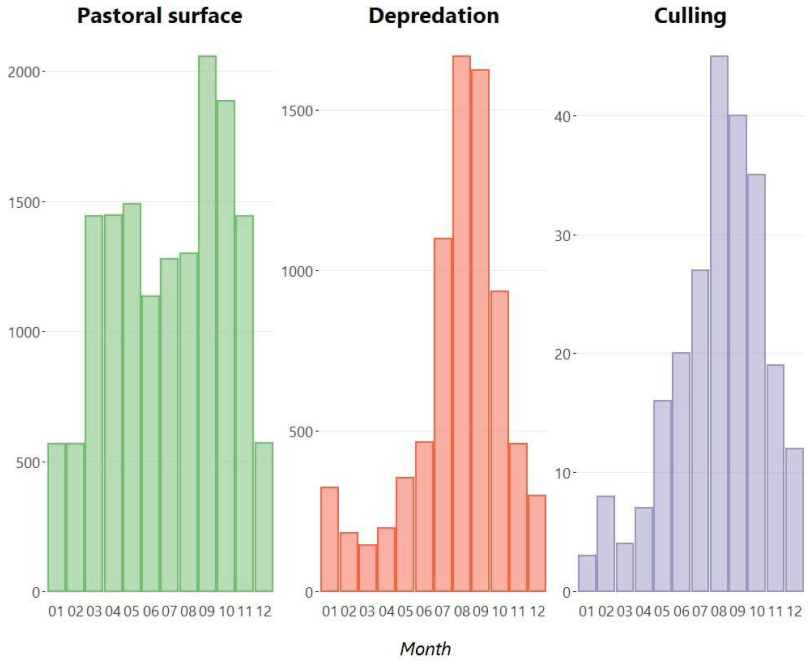


Figure 3.29: Distribution of the month frequency of use of the pastoral surfaces within the spatial buffers of the 236 unique culling events (left), of the month frequency of depredations of these buffers (middle) and the month frequency of the 236 unique culling events. Credits: O. Grente

Without surprise, the seasonality was high for depredations, with a peak in August and September. The culling event peak followed the depredation peak, but culling events were more frequent in October than in June, contrary to the depredations. The pastoral surfaces which were part of the spatial buffers of the culling events were more used during September and October, and weakly used in winter, from December to February.

For a culling event occurring in October, the 90-day period of its buffer overlapped the period from November to January, when pastoral surfaces were mostly not used. For such culling events, the time correction could therefore play its full role.

Problem statement

If the conditions (pastoral, environmental...) were unalterable in time, then the differences in the depredation intensity before and after the culling effects should be enough to observe the effects of such culling. However, as said in section *Analysis*, this was not true. The depredation intensity dynamic could changer over time because:

- **The culling event**: this was the effect on which we were focused. The culling event could have eliminated the wolf or wolves causing the depredations, and/or modified the depredation behaviour of the surviving wolves.

- **The livestock**: the main cause being the arrival and departure of flocks from the pastures. The pastoral practices could also have been changed over time. This was a confounding effect.
- **The wolves**: the wolves have an annual reproductive cycle (Chapter 1). In summer, the food needs of the pack increase because of the growth of pups. In autumn, the pups start to integrate the hunting groups, and a dispersal of subadults can happen. The autumnal dispersal could decrease the pack food needs, and therefore the risks for depredation (Chapter 2). This was a confounding effect.
- **Environmental factors**: The wild prey reproductive cycles could have an impact on the depredation risks (Chapter 2). This was a confounding effect.

We needed to extract or at least to estimate the depredation dynamic without culling for the pastures concerned by the analysis. Then, the difference of the two dynamics, the one with culling (from Figure 3.28) and the one without culling would allow us to observe the culling effect corrected for the seasonal bias (*i.e.* the confounding factors due to time). But the question was: *how did we get the depredation dynamic without culling?*

Ideally, we could control for all these factors. However, it was not possible here because we worked with data already compiled. We had to find other ways to deal with the confounding factors due to time. We developed three complementary methods:

- *Method 1: restriction of the temporal buffer*. We decreased the risks of confounding factors due to time by drastically reducing the temporal buffer.
- *Method 2: estimated pastoral dynamic*. We corrected the depredation intensity with an estimation of the pastoral use intensity.
- *Method 3: estimated seasonal dynamic without culling*. We estimated the seasonal dynamic of depredations without culling for close areas in space and time to the culling buffers.

Method 1: restriction of the temporal buffer

This method was the simplest one. The spatio-temporal buffers were here changed by reducing the time period of the buffers. This way, it was possible, when considering the effect of culling on a short time, to limit the risks for the confounded factors listed above to change.

Reducing the time period of the buffers had several consequences on the construction of the buffers and the kernel estimation. Here are listed the changes that happened:

- *Spatio-temporal limits of the buffer:* We chose here a temporal limit of 20 days before and 20 days after the culling events, therefore **40 days** in total. The spatial limit was unchanged, and remained at 10 km around the culling events (buffers of **20 km** of diameter).
- *Limit date of the analysis:* Because the temporal limit was reduced, the limit date of the analysis for the culling events was delayed to the **12th December 2020**. Thus, no culling event had to be put aside from this analysis because of its date.

- *Interactions between buffers:* The definition of the limit between low and high spatial and temporal risks of interaction between pairs of overlapping buffers were not changed and remained at **5 km** and **25 days** between the culling events. Thanks to the last step, there were more culling events to be analysed at this point, increasing the risks for overlapping buffers. However, the spatio-temporal buffers were smaller now thanks to the smaller temporal limit, therefore decreasing the risks for overlapping buffers. At the end, 110 culling events were considered as having high risks of spatial and temporal interaction between buffers, nearly as many as previously.
- *Buffer finalisation:* In total, **252 unique culling events with a shorter temporal buffer were analysed**.
- *Kernel estimation:* The smoothing parameter of the temporal axis had to be adapted to the shorter analysed time period. It was changed to **0.5 day** instead of 2.

The results are given in Figure 3.30 (see Appendix C.1 for the raw results with outliers).

Results were quite similar to the those obtained with a temporal buffer of 180 days (Figure 3.28). As previously, high depredation values could be found before and after the culling events. High depredation density values were mostly spatially aggregated towards the culling event location, except for some peaks within 5 km before the culling event (Figure 3.30). The results did not show depredation reports around the culling events either.

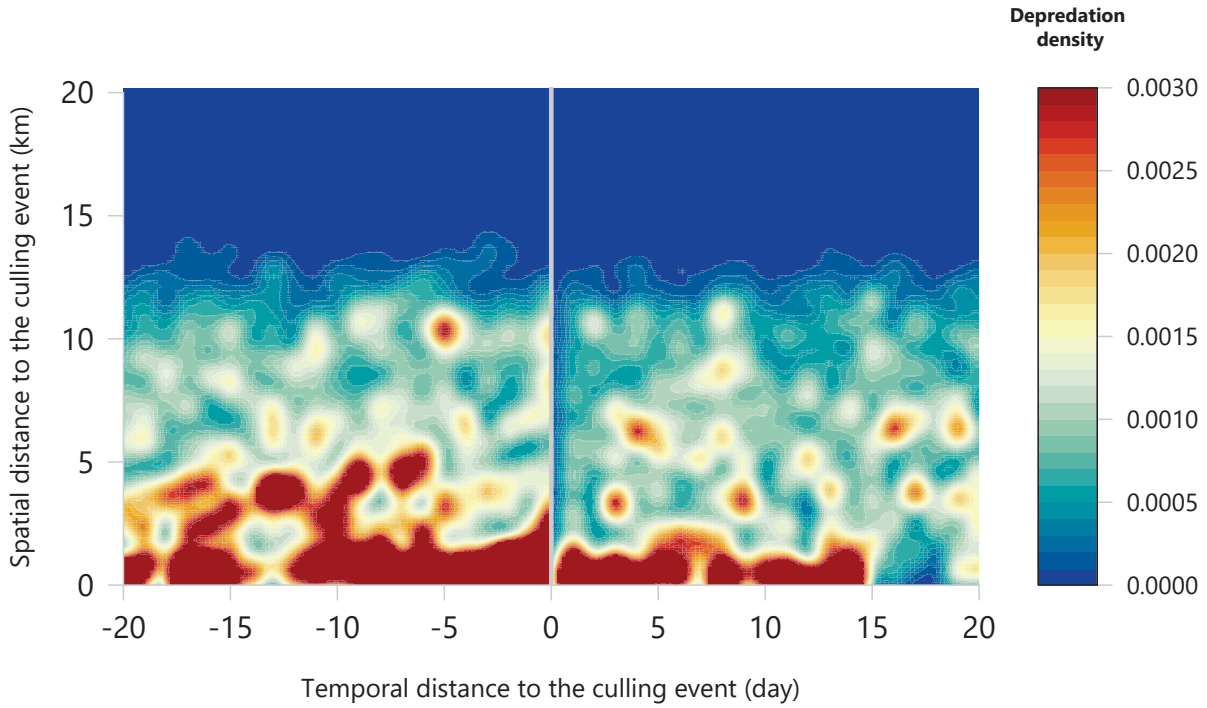


Figure 3.30: Estimation of the depredation density per unit of time and space around the 252 unique culling events with a temporal buffer of 40 days. The highest density values were brought to the outlier threshold. The depredation density of a unit was defined in Definition 4. The depredations involved in the analysis were found inside the pastures partially or integrally overlapping the circle of 10 km radius around the culling events. Depredations were therefore scarcer above 10 km from the culling events, as the pastures were generally not spread out over large distances outside the circle of 10 km radius. Credits: O. Grente

Reducing the temporal buffer...

- To 40 days instead of 180 days,
- did not produce large differences with the previous results,
- but increased the culling analysed dataset of culling events,
- and decreased the risks for confounding factors due to time.

Method 2: estimated pastoral dynamic

This method had the aim to estimate the pastoral use within the spatio-temporal buffers of the 236 unique culling events. The spatio-temporal use of pastoral surfaces was the only one available data among the set of confounding factors due to time. In addition, the seasonality induced by pastoral seasonality probably produced the highest risks of analysis bias among the set of confounding factors. By correcting the depredation intensity with the pastoral intensity, it was possible to limit the risks of confounding factors due to the pastoral seasonality, and to analyse the culling effect over 180 days.

During the construction of the 236 spatio-temporal buffers, we had extracted the pastoral surfaces within the spatial buffers (section *Limit space of the analysis*). For these sets of pastoral surfaces (one set for each buffer), we had to know how many months they were used for sheep grazing during the time period covered by the buffers. Let's call this number the '*pastoral weight*'.

Similarly to the spatial correction in section *Transition from 3D to 2D*, which was dependent on pastoral data, we could have applied a temporal correction to the depredation events. Indeed, we could have lowered the weight of a depredation in the analysis because it was found during of period of high pastoral use.

However, the pastoral correction should not have been dependent on the observed depredation intensity. Indeed, with such a correction, the corrections could only have been applied for the observed depredations. If there was no depredation in a specific unit in the final kernel, therefore there was no way to know, with the previous correction, if it was a unit corresponding to a high pastoral use or not.

A better way to correct the depredation intensity by the pastoral intensity was to produce a correction which had the same kernel format. Thus, it would be easy to calculate the difference between the kernel estimations of the observed depredation intensity, and the kernel estimations of the pastoral use intensity. To this end, **we simulated a dummy set of depredations randomly located in space and time according to the pastoral space and the use of this space by sheep in time**. Thus, we were able to apply kernel estimations on these simulated depredations.The simulated densities reflected the pastoral use in space and time.

To produce this set of simulated depredations, we applied the following steps for each culling event, and therefore for each buffer:

1. *Extract the spatio-temporal pastoral use.*
    a) We sliced the spatial buffer into the same 200 rings of progressive radius as those in section *Transition from 3D to 2D*. Let's call one ring j. We also sliced the temporal buffer of 180 days into 200 classes; each class represented a duration of $\frac{180}{200} = 0.9$ day. Let's call one time class i.
    b) The sum of the pastoral area in use was computed for each ring j at each time class i. Contrary to what was done in section *Transition from 3D to 2D*, a pastoral surface crossed by the ring j but not in use (according to the IRSTEA information) during the month of time class i did not count for the sum calculations.
    c) We ended up with a matrix $[i; j]$ of the pastoral area in use for the given buffer.
2. *Simulate the depredations.*
    a) A set of coordinates $[i; j]$ was drawn from our previous matrix. The number of drawn coordinates equalled the number of observed depredations for the given buffer. The probability for a set of coordinates to be drawn was equal to its pastoral area in use (rescaled from 0 to 1).
    b) The spatial correction for each set of coordinates $[i; j]$ was computed following the same methodology as in section *Transition from 3D to 2D*.
    c) The previous step was done 1000 times.
    d) We ended up with 1000 sets of coordinates $[i; j]$, each set representing the time and space locations of the depredations simulated for the given buffer.

We had now to associate the simulated sets of coordinates $[i; j]$ of the 236 buffers. To this end, we compiled 236 simulated sets of coordinates, one for each buffer. The compilation was done until all sets of coordinates had been used. Thus, we ended with 1000 simulated sets of coordinates, each set representing the time and space locations of the depredations simulated for all the 236 buffers.

The kernel estimation was done for each of the 1000 simulated sets of coordinates, following the same methodology as in section *The kernel estimation*. The result was 1000 matrices of the depredation density, each matrix representing the depredation density simulated for all the 236 buffers. The idea was not to compare the kernel estimation of the observed depredations with the 1000 simulated matrices one by one. It was necessary to average the 1000 simulated matrices into a unique one: **the averaged matrix of simulated depredation density**.Because simulations were subjected to stochasticity, we also computed the standard deviations of the 1000 simulated matrices (results in Appendix C.2).

The results of the averaged matrix of simulated depredation density are given in Figure 3.31. There was no outlier correction required for the simulations. We noticed that the simulated depredation density scale was close to the observed depredation density scale from Figure 3.26.

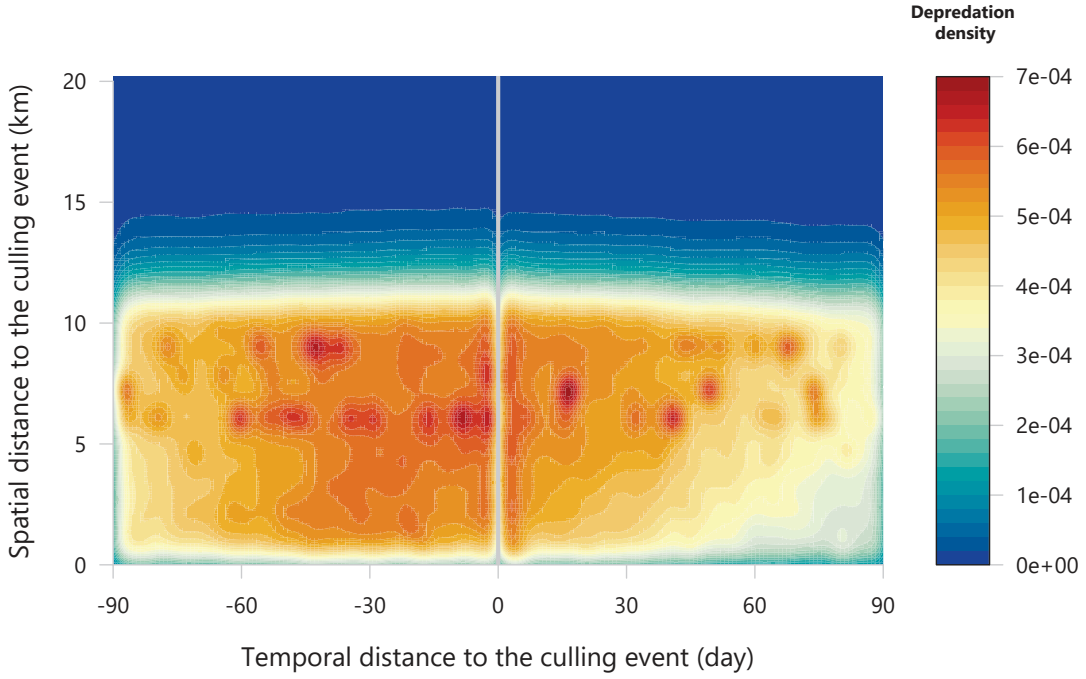


Figure 3.31: The averaged matrix of simulated depredation density for the 236 unique culling events, when simulating 1000 sets of depredations spatially and temporally located according to the pastoral use. Credits: O. Grente

Let's compare the results of Figure 3.31 to the observed depredation densities shown in Figure 3.28. Despite the use of spatial correction, the simulated depredation intensity showed higher values farther from the culling event spatial location than the observed depredation density. The simulated high densities were mostly located around 5 km but were spread out across the spatial area covered by the buffers (at the exception of the distances larger than 10 km where few pastoral area was represented in the analysis). However, you can notice that the high simulated densities were mostly located before the culling events, and were lowering as we moved forward in time after the culling events. Precautions were required when considering the very located peaks of highest mean density values (7e-04), as they matched with the highest standard deviation values (Appendix C.2). This meant that they were areas of high variability among the simulations.

Thus, **the simulated depredation densities from Figure 3.31 were the expected depredation densities given the pastoral use**. We corrected the observed depredation intensity with this estimated pastoral intensity, by applying Equation 3.2:

$$\lambda_{cor}[i;j] = \lambda_{obs}[i;j] - \lambda_{sim}[i;j] \quad (3.2)$$

where $\lambda_{cor}[i;j]$ was the corrected depredation density value at the set of coordinates $[i;j]$, $\lambda_{obs}[i;j]$ was the observed depredation density value at the set of coordinate $[i;j]$ (from Figure 3.28) when the analysis included both spatial and outlier corrections, and $\lambda_{sim}[i;j]$ was the simulated depredation density value at the set of coordinate $[i;j]$ (from Figure 3.31).

Thus, a value of zero resulting from Equation 3.2 meant that there was as much depredation density as expected according to the pastoral use. A value higher than 0 indicated there was a higher depredation density than the one expected according to the pastoral use. It was the opposite for values lower than 0. The result of this correction is given in Figure 3.32.

The temporal correction applied in Figure 3.32 showed that the highest values of depredation density were still found near the location of the culling events. The correction decreased the values that were further from the culling event spatial locations, as expected given the results of the depredation simulations in Figure 3.31.

The depredation density was high before the culling events over a long period of time, approximately during 60 days. The depredation density was higher after the culling events (especially with increasing time distance) but these high values were occurring on much more shorter periods of time than those before the culling events. These high values were also more restricted towards the culling spatial location (< 2 km) compared to the high values encountered before the culling events.

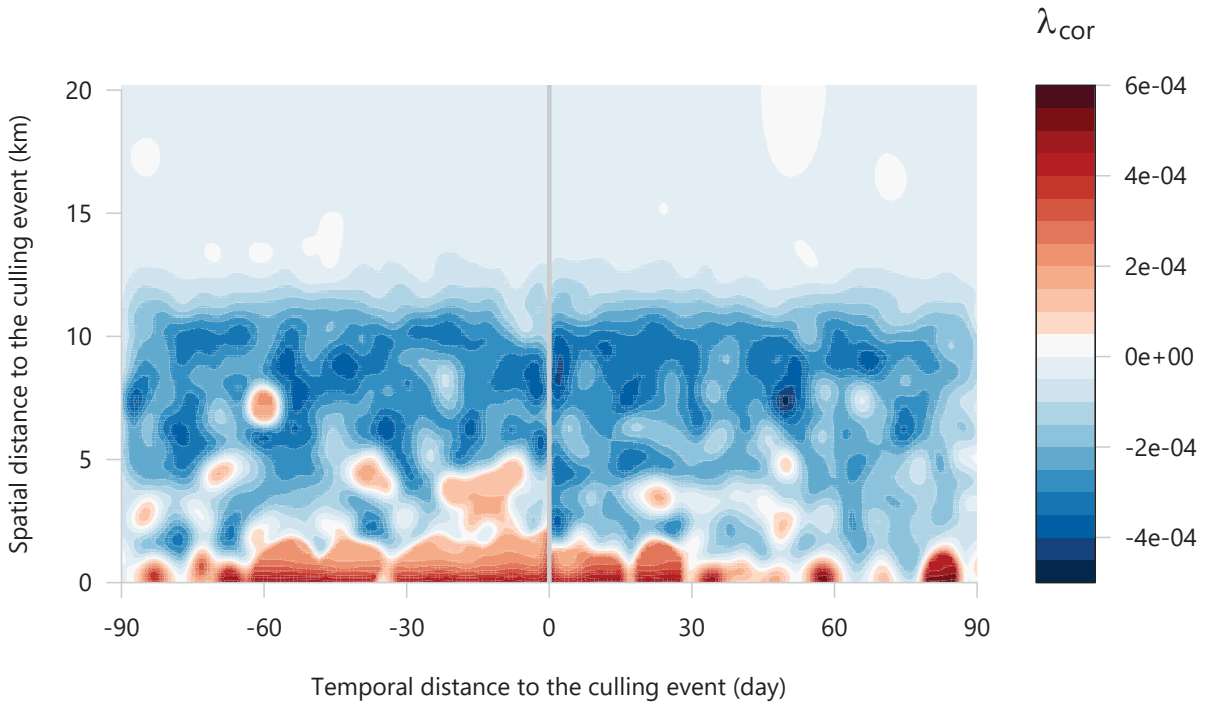


Figure 3.32: Estimation of the differences between the observed depredation density, with outlier corrections included, and the depredation density expected according to the pastoral use, for the 236 unique culling events. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

Estimating the pastoral use...

- allowed us to correct for the temporal bias induced by the pastoral dynamic,
- reinforced the depredation density after the culling events compared to the result without correction;

- This corrected density could be higher after than before the culling events,
- but this high density was running over periods of time that were shorter after the culling events compared to before.

Method 3: estimated seasonal dynamic without culling

This third and last method had the aim to correct the observed depredation intensity in the buffers of the 236 unique culling events by the seasonal dynamic of depredations without culling.

Except the spatio-temporal use of pastoral surfaces, we had no available data about the set of confounding factors due to time. To estimate the seasonal dynamic of depredations caused by the whole set of confounding factors, we needed to identify equivalent spatio-temporal areas to the 236 analysed buffers, but where no culling could influence the depredation intensity dynamic. This way, we could expect that the confounding factors would behave the same way in the similar buffers that in the observed buffers. The depredation intensity of these buffers without culling would therefore be an approximation (or a '*proxy*') for the depredation seasonal dynamic without culling. We called the centre of these buffers the '*non-culling*' events, as they represented a point in space and time where no culling was applied.

For each of the 236 buffers of unique culling event, the extraction of the corresponding non-culling event followed these conditions:

- **The non-culling event should be located within the same zone of the corresponding observed culling event.** This was intended to provide spatial environmental constraints similar to the observed culling event. We used the work of Nivologie des Alpes du Sud which defined 25 Alpine massifs based on hydrography and orography. We combined to these 25 massifs two supplementary zones of interest for our study, the Parc Naturel Régional des Préalpes d'Azur and the Canjuers military camp, delimited by OpenStreetMap. Most observed culling events were within these 27 zones (Figure 3.33 and Figure 3.34). For the 227 observed culling events located at less than 15 km from these zones, we attributed their non-culling events to the closest zone. The 9 observed culling events, farther than 15 km from their closest zone, were excluded from this analysis.
- **The dates of the non-culling event was randomly chosen in a period of 40 days surrounding the date of the observed culling event (20 days before and 20 days after).** This was intended to provide temporal environmental constraints similar to the observed culling event.
- **The spatio-temporal buffer of a non-culling event could not interact with the spatio-temporal buffers of any of the 362 known culling events.** We used the same criteria of interactions than in section *Interactions between buffers*: 25 days and 5 km. This was intended to extract the depredation dynamic without the influence of culling.

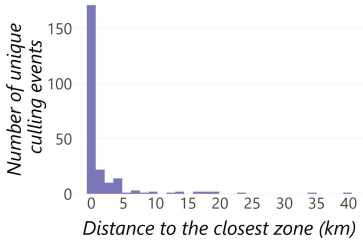


Figure 3.33: Distance of the observed unique culling events to their closest zone, amongst the 27 zones presented in Figure 3.34. Credits: O. Grente

For each unique culling event, we could not approximate the depredation dynamic without culling based on only one non-culling event. We had to identify a large amount of non-culling events, in order to extract a large amount of depredation dynamics without culling. Thus, for each observed culling event, we identified 100 corresponding non-culling events[13], produced according to the above conditions.

13: This number is 10 times smaller than in method 2 because of computational times, the calculations of the spatial corrections for each buffer being time-consuming.

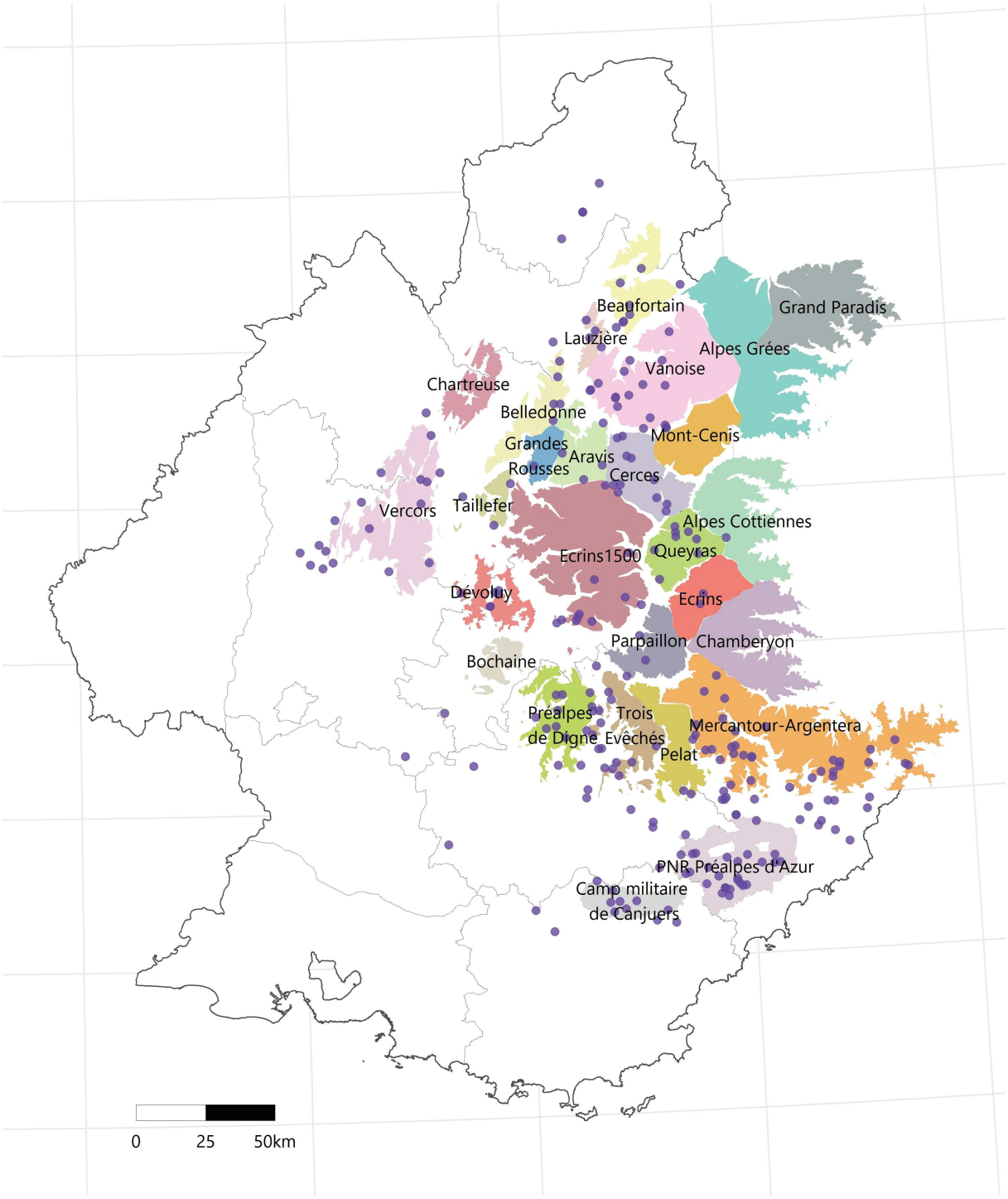


Figure 3.34: Map of the 25 Alpine massifs delimited by Nivologie des Alpes du Sud and the Parc Naturel Régional des Préalpes d'Azur and the Canjuers military camp. The purple points represents the 236 observed unique culling events. Credits: O. Grente

To produce the final correction, we followed the same methodology than in method 2. We compiled, in one single set, 227 non-culling events, each one representing the non-culling event corresponding to one observed culling event. The compilation was done until all non-culling events had been used. Thus, we ended with 100 sets of non-culling events, each set representing the time and space locations of the non-culling events simulated for all the 227 observed culling events.

Then, we constructed for each non-culling event a buffer of 20 km of diameter and lasting 180 days around the non-culling event, similarly to the buffer of the observed culling events. There was no need here to remove the interacting non-culling events, as there were supposedly no influence of culling for any of these buffers. The spatial correction for each depredation of each non-culling event buffer was then calculated, following the previous methodology applied for the observed culling events and explained in section *Transition from 3D to 2D*. The final step of buffer construction and the kernel estimation were applied following the same methodologies as the ones applied for the observed culling events, as explained in section *Buffer finalisation* and in section *The kernel estimation*.

We then ended with 100 kernel estimations, each one representing the estimation of one set of non-culling events. As in method 2, it was necessary to average the 100 kernel estimations into a unique one: **the averaged depredation density of the non-culling events**. As previously, we also computed the standard deviations of the 100 kernel estimations (results in Appendix Figure C.3).

The results of the averaged depredation density of the non-culling events are given in Figure 3.35. A correction for outliers was required, as for the observed culling events. See Appendix Figure C.4 for raw results with outliers.

The upper limit of the depredation density scale when using the non-culling events was 1.6 higher than the upper limit when using the 227 observed culling events retained for this analysis[14].

Let's compare the results of Figure 3.35 to the observed depredation densities shown in Figure 3.28. With the non-culling events, the depredations were particularly intense right after the culling events, and close to them in space. Before the culling events, the depredations were intense up to 20 days before these events, but on shorter periods of time compared to the intense spot after the culling events. However this high spot of intensity after the culling events matched with the highest standard deviation value (Appendix Figure C.3). This meant that the spot was an area of high variability among the simulations. This could be due to the limited number of simulations we used for this method.

14: The kernel estimation for the 227 observed culling events retained for this analysis provided very similar results to Figure 3.28, where the whole set of 236 unique culling events was taking into account.

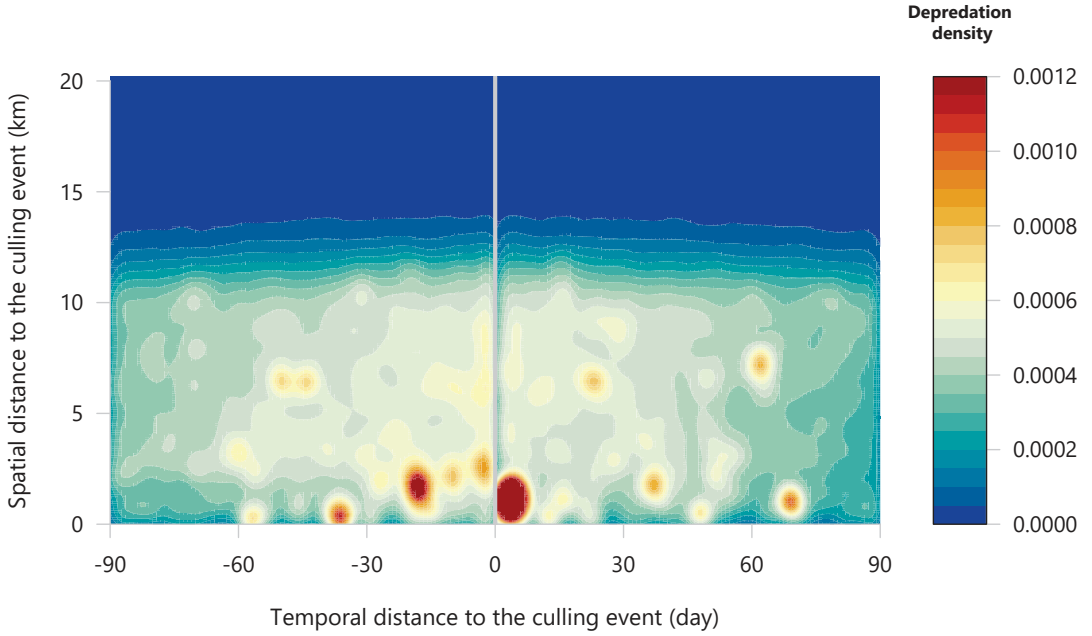


Figure 3.35: Estimation of the mean depredation density for 100 sets of 227 non-culling events. Each set of 227 non-culling events was selected to involve equivalent confounding factors to those of the observed set of 227 unique culling events. The outlier correction was applied. Credits: O. Grente

Then, we applied the same type of correction as in method 2, with Equation 3.3:

$$\lambda_{cor}[i;j] = \lambda_{obs}[i;j] - \lambda_{proxy}[i;j] \tag{3.3}$$

where $\lambda_{cor}[i;j]$ was the corrected depredation density value at the set of coordinates $[i;j]$, $\lambda_{obs}[i;j]$ was the observed depredation density value at the set of coordinate $[i;j]$ for the 227 observed unique culling events, corrected with spatial and outlier corrections, and $\lambda_{proxy}[i;j]$ was the approximated depredation density value without culling at the set of coordinate $[i;j]$ from Figure 3.35.

Thus, a value of zero resulting from Equation 3.3 meant that there was as much depredation density as expected according to the estimated seasonal dynamic of depredations without culling. A value higher than 0 indicated there was a higher observed depredation density than the one expected according to the estimated seasonal dynamic of depredations without culling. It was the opposite for values lower than 0. The result of this correction is given in Figure 3.36.

The temporal correction applied in Figure 3.36 showed that the highest values of depredation density were still found near the culling events. The most noticeable effects of this correction was the low negative values encountered right after the culling events over ~ 5 days. This was due to the spot of high depredation intensity found in Figure 3.35. **Because of the high incertitude regarding this spot relatively to the low number of simulations, we decided to select the pastoral correction from section *Method 2: estimated pastoral dynamic* thereafter.**

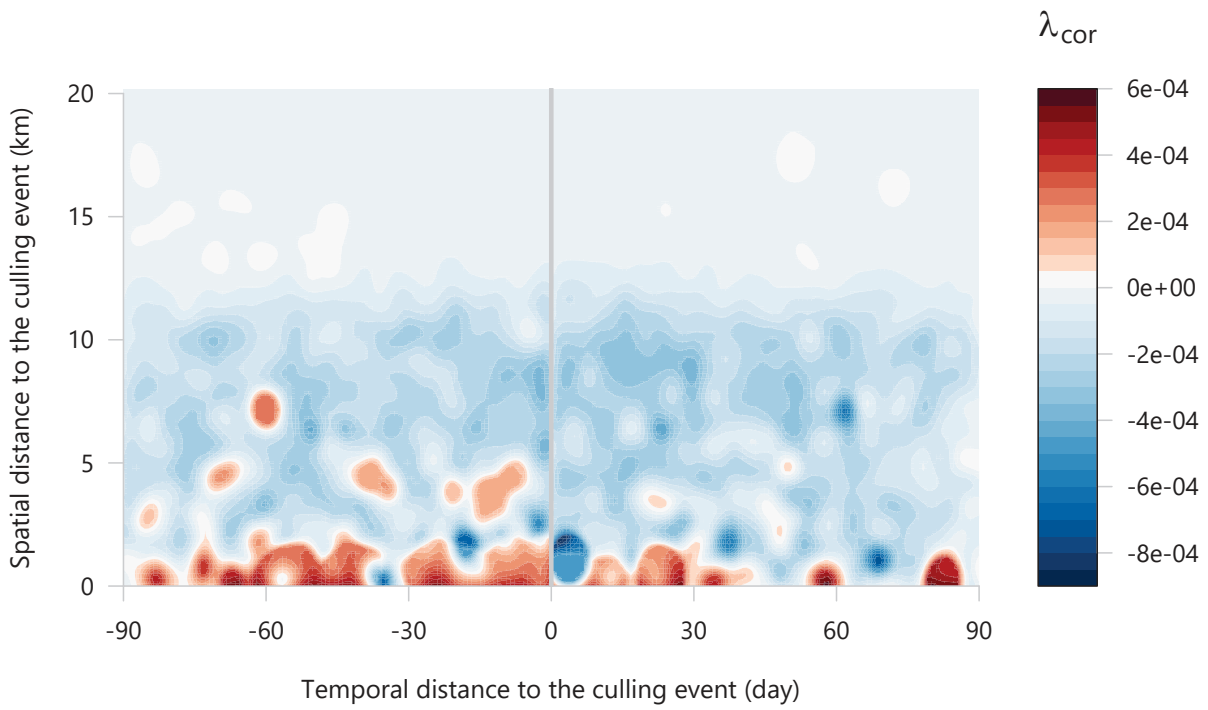


Figure 3.36: Estimation of the differences between the observed depredation density, with outlier corrections included, and the depredation density expected according to the estimated seasonal dynamic of depredations without culling, for the 227 unique culling events retained for the analysis. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the estimated seasonal dynamic of depredations without culling. Credits: O. Grente

Estimating the seasonal dynamic without culling...

- was done through a simulation of '*non-culling events*' that were selected to have a similar contexts to the real culling events,
- was based on the spatial delimitation of massifs,
- but implied long computational times,
- and too high variations among simulations,
- which led us to prefer the pastoral correction to this one, in order to correct temporal biases.

Variability of the culling effects

As mentioned previously in section *Clues for interpretation*, the general tendency could mask the effects of some culling events. **We therefore investigated the variability of the culling effects by separately analysing the culling events according to their characteristics**.

However, to be able to divide the analysis of the culling events according to their characteristics, the number of culling events within categories should not be too unbalanced. A good example is the age of the culled wolf. For the 236 unique culling events that were analysed, 153 culled wolves were categorised as adults, 21 as subadults and 8 as pups (the rest was unknown). The imbalance between these three categories meant that the analysis of the culling events with adult wolves would have led

to results close to the general results, and the comparison with the two other categories would have been complicated.

Taking this constraint into consideration, we analysed the variability of the culling effect according to four main variables:

1. The location of the culling events, according to two classes:
   - The location within massifs
   - The altitude
2. The season of the culling events, according to the wolf biology
3. The types of culling authorisation (defence, harvest)
4. The sex of the culled wolf

For each category of each variable, the whole analysis previously presented was identically re-done with the culling events of this category. To correct for temporal biases, we chose Method 2, with the pastoral correction (with a minor change*), for the reasons previously explained. **Only the kernel figures with the spatial correction, the outlier correction and the pastoral correction are presented below.**

***Minor change**

Contrary to the results with the whole set of 236 unique culling events, the simulated density scales of Method 2 were not always similar to the observed depredation density scales (corrected for outliers) when analysing the culling events per category. To avoid that the pastoral correction flattens the observed depredation intensities or vice-versa, **we rescaled the intensities of the pastoral correction according to the range of the observed intensities (corrected for outliers)**, following Equation 2.1 previously used in Chapter 2.

Massifs

In this section, we investigated the culling effect according to the location of the culling events within zones or massifs (Figure 3.34). We used the same 227 culling events as those used in section *Method 3: estimated seasonal dynamic without culling* (*i.e.* we excluded the culling events too far from massifs). The culling events were not evenly distributed within massifs (Figure 3.37). They were predominantly in the Alpes-Maritimes department, within the massif *Mercantour-Argentera* and the *Regional Park Préalpes d'Azur*.

Keep in mind

In the following results, I will describe the observed variations of the *'depredation intensities'*. To be more rigorous, I should rather use the terms *'the differences between the observed depredations intensities and those expected according to pastoral use'*, symbolised by λ_{cor}. However I thought it would facilitate the reading to use this abridged version.

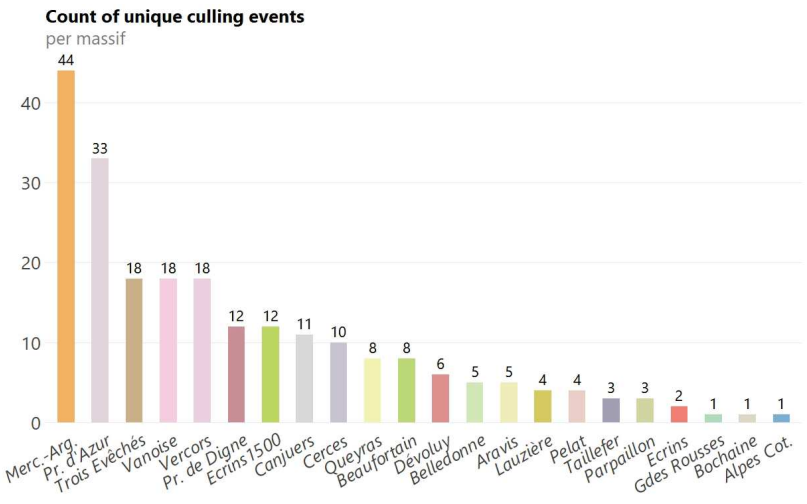


Figure 3.37: Distribution of the culling events within massifs, of which the delimitation comes from the work of Nivologie des Alpes du Sud to which we added the Parc Naturel Régional des Préalpes d'Azur and the Canjuers military camp, delimited by OpenStreetMap. Credits: O. Grente

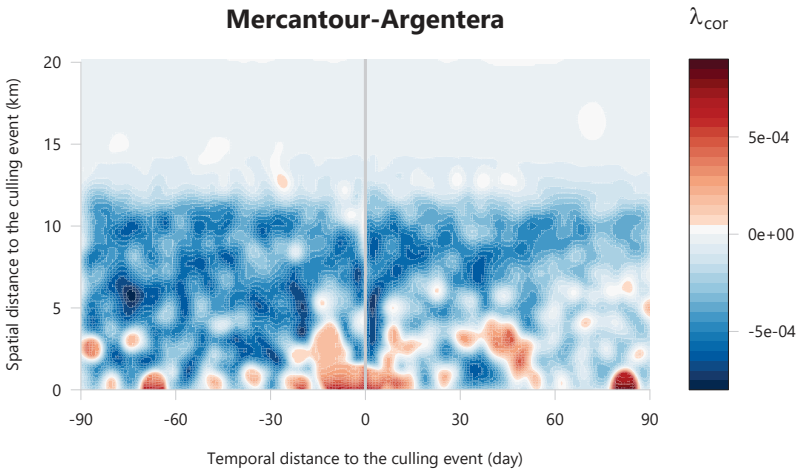
Let's apply our developed methodology for each massif, from the one with the highest number of culling events to the lowest. Nevertheless, we excluded from the analysis the massifs with less than 10 culling events, to avoid investigation on a too small number of culling events.

► Mercantour-Argentera

Depredation intensities were almost vertically symmetrical around the culling events line at $x = 0$, from -30 to 30 days, suggesting **no effect of the culling events on a short period**. However, a spot of high intensities of depredations at 4-5 km and at 30 days, which came closer to the event location with time, had no equivalent before the culling events. This could **suggest a report of depredation**. The highest depredation intensity spot was also found after the culling events, on a short period of time and close to the event location, but at the limit of the study period.

Analysed data

There were 44 unique culling events within the massif Mercantour-Argentera. Their buffers encompassed on average 62 depredations ($sd = 38$) for a total of 2 717 depredations.



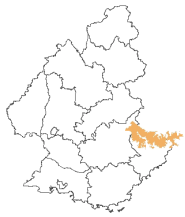


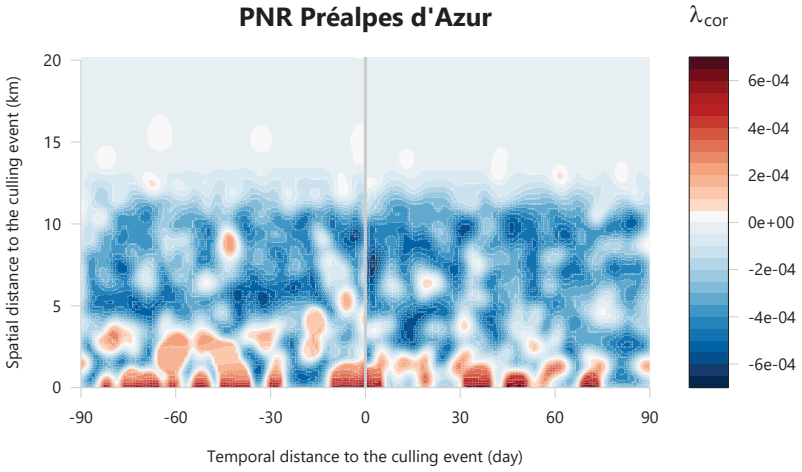
Figure 3.38: Depredation density corrected by pastoral use for the 44 unique culling events in Mercantour-Argentera. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► PNR Préalpes d'Azur

Depredations still occurred after the culling events. The intensities were slightly higher after the culling events, but less spread out over space compared to before these events. **It is therefore difficult to conclude on the culling effects for this area**.

Analysed Data

There were 33 unique culling events within the Regional Park Préalpes d'Azur. Their buffers encompassed on average 44 depredations ($sd = 22$) for a total of 1 441 depredations.



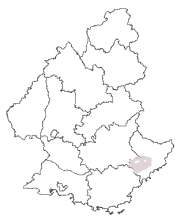


Figure 3.39: Depredation density corrected by pastoral use for the 33 unique culling events of the Regional Park Préalpes d'Azur. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Trois-Evêchés**

The kernel Figure 3.40 showed **an overall reduction of depredation intensity after the culling events**. Depredations close to the location of the culling events only persisted a few days right after the culling events, and tended to be found a bit farther, between 1–2.5 km. Between 20–30 days and around 5 km, high intensities appeared. It could potentially **suggest a spatial report of depredation**.

Analysed Data

There were 18 unique culling events within the massif Trois-Evêchés. Their buffers encompassed on average 26 depredations (sd = 23) for a total of 475 depredations.

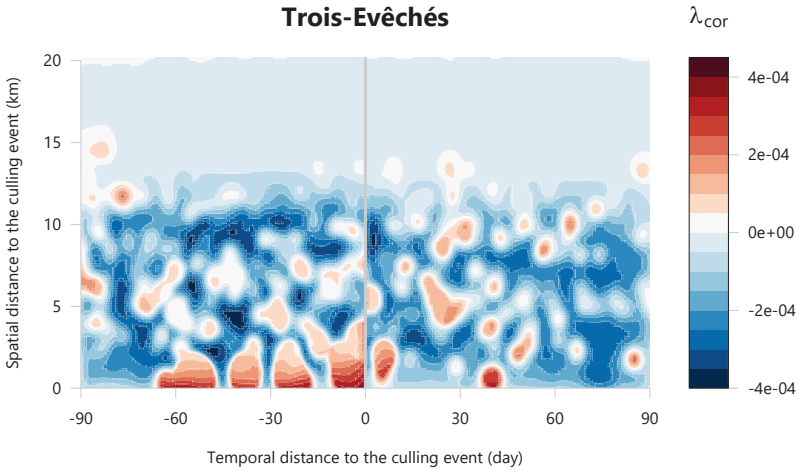




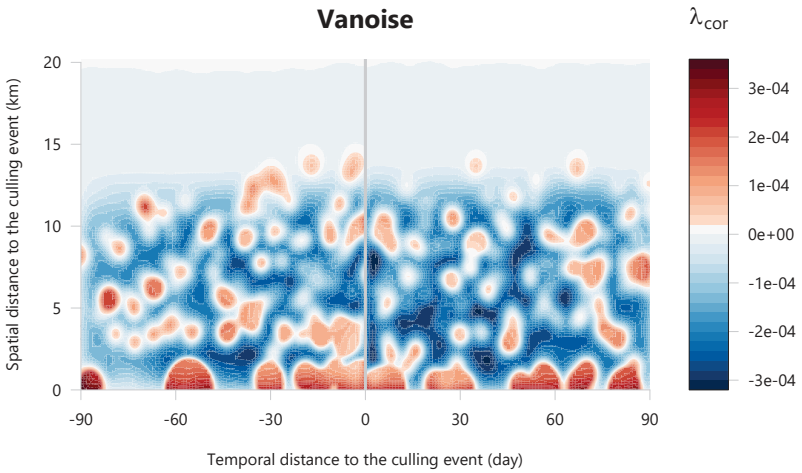
Figure 3.40: Depredation density corrected by pastoral use for the 18 unique culling events of the massif Trois-Evêchés. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Vanoise**

The kernel Figure 3.41 showed results that were almost vertically symmetrical around the culling events line at $x = 0$. Therefore, **the culling events in this massif did not seem to an have effect on the depredation intensities**. No spatial spread or report was suspected.

Analysed Data

There were 18 unique culling events within the massif Vanoise. Their buffers encompassed on average 19 depredations (sd = 12) for a total of 338 depredations.



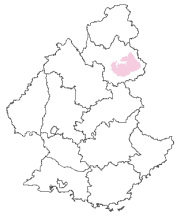


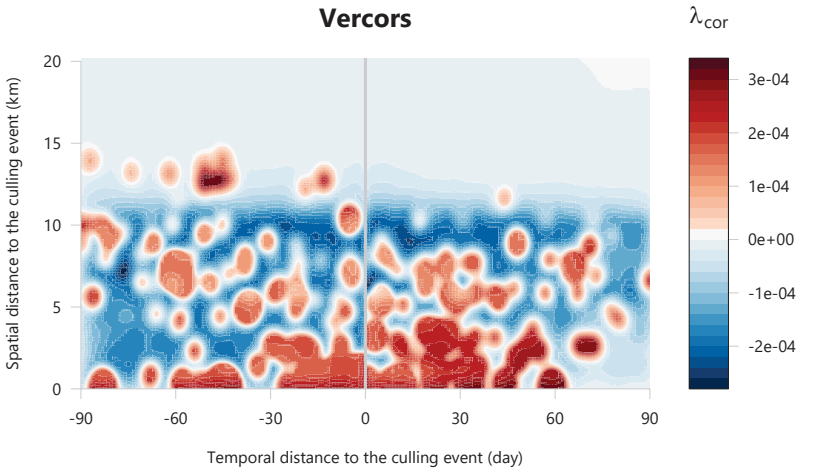
Figure 3.41: Depredation density corrected by pastoral use for the 18 unique culling events of the massif Vanoise. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Vercors**

The kernel Figure 3.42 showed that **the overall depredation intensity increased after the culling events**, and were more spread out over space, **suggesting a potential spread of depredations**.

Analysed Data

There were 18 unique culling events within the massif Vercors. Their buffers encompassed on average 11 depredations ($sd = 7$) for a total of 202 depredations.



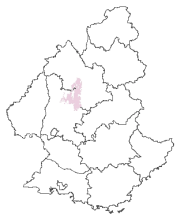


Figure 3.42: Depredation density corrected by pastoral use for the 18 unique culling events of the massif Vercors. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Préalpes de Digne**

The kernel Figure 3.43 showed a **brutal reduction of depredations right after the culling events without depredation recurrence over 90 days at proximity of the culling events** (at the exception of a short phase around 40 days at 0–1 km). The contrast was marked because the high depredation intensity found before the culling events was continuous from -80 days to the date of the culling events and spread to 2 km at least from the events. However, the spots of depredations found beyond 5 km after the culling events were also present at the same distances before the events but with more intensity: this could **suggest a spatial report of depredation** due to the culling events.

Analysed Data

There were 12 unique culling events within the massif Préalpes de Digne. Their buffers encompassed on average 19 depredations ($sd = 7$) for a total of 232 depredations.

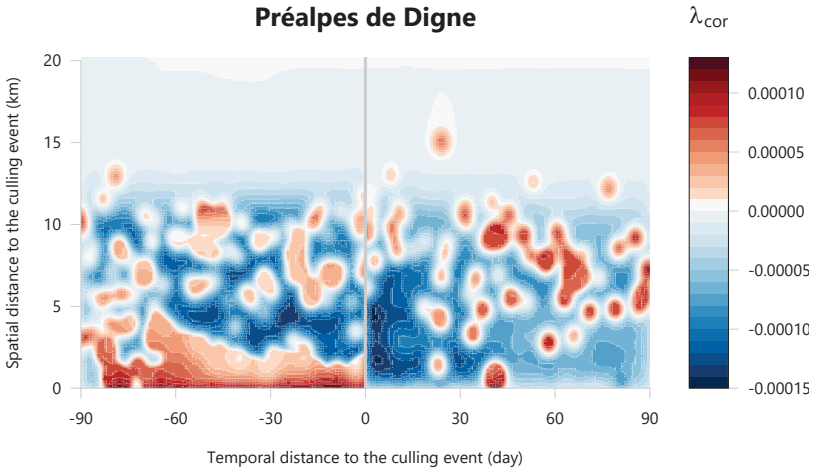




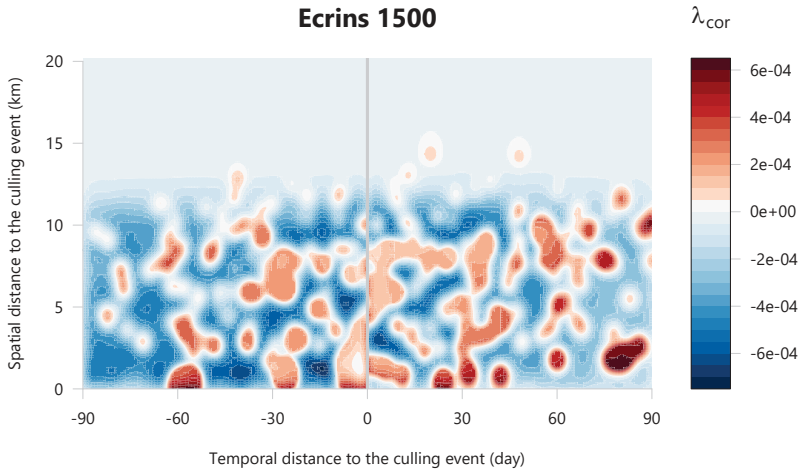
Figure 3.43: Depredation density corrected by pastoral use for the 12 unique culling events of the massif Préalpes de Digne. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Ecrins 1500**

Immediately after the culling events, the **depredations were still present**, but seemed mainly reported above 5 km from the events. Moreover, spots of high depredation intensity over short periods of time occurred after the culling events, at various distances (like before the events) up to 90 days after the events, with intensity increasing as time passed after the events.

Analysed Data

There were 12 unique culling events within the massif Ecrins 1500. Their buffers encompassed on average 27 depredations (sd = 14) for a total of 321 depredations.



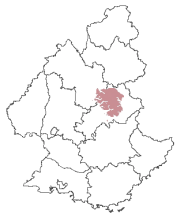


Figure 3.44: Depredation density corrected by pastoral use for the 12 unique culling events of the massif Ecrins 1500. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Canjuers**

The kernel Figure 3.45 showed no change in the depredation intensities when comparing over a period of 30 days before and after the events. The period of high intensity close to the events was even longer after the events than before. However, there were spots of high depredation intensities around -60 days that were not found at +60 days. It is therefore **difficult to conclude on the culling effects in Canjuers**.

Analysed Data

There were 11 unique culling events within the massif Canjuers. Their buffers encompassed on average 61 depredations (sd = 28) for a total of 672 depredations.

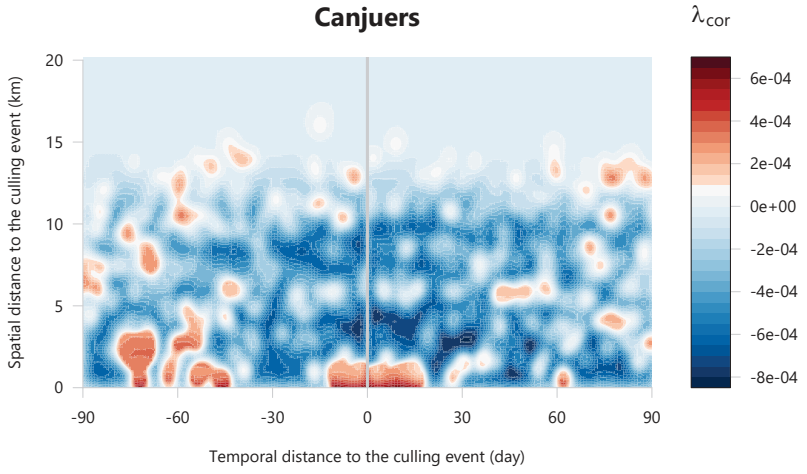




Figure 3.45: Depredation density corrected by pastoral use for the 11 unique culling events of the massif Canjuers. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► Cerces

The kernel Figure 3.46 showed **a clear reduction of depredation intensity right after the culling events and close to their locations**. However, spots of high depredations were nonetheless present after the events, at various distances. Even if they were present at these distances before the events too, the depredations were not as intense as they were after the culling events. This could be signal for a depredation report. Depredation recurrence at the locations of the culling events was observed 55 days later, with higher depredation intensity than what was observed before the events.

Analysed Data

There were 10 unique culling events within the massif Cerces. Their buffers encompassed on average 13 depredations (sd = 7) for a total of 129 depredations.

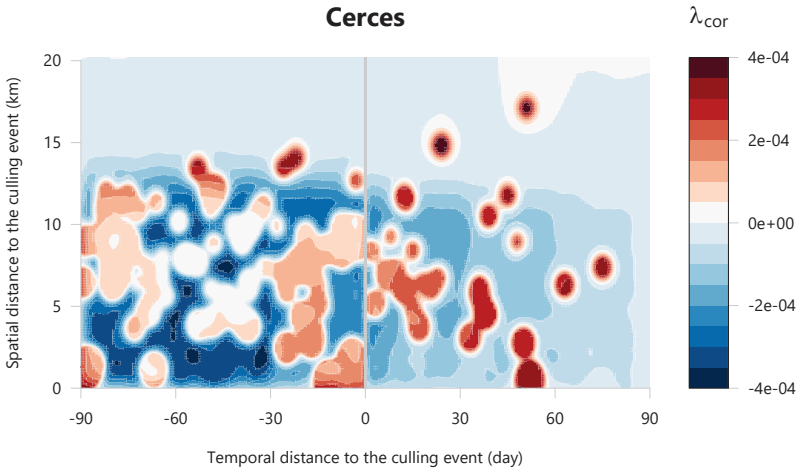




Figure 3.46: Depredation density corrected by pastoral use for the 10 unique culling events of the massif Cerces. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

Altitude

In this section, we investigated the culling effect according to altitude zones (Figure 3.34). We used the whole set of 236 culling events. The culling events were not evenly distributed within massifs (Figure 3.37).

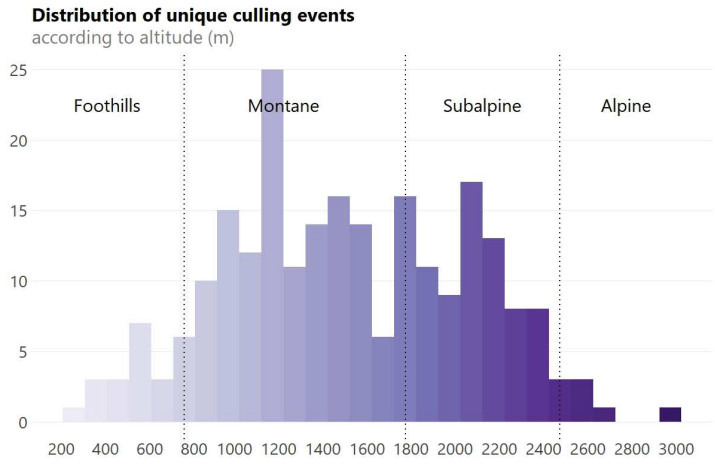


Figure 3.47: Distribution of the 236 culling events according to classes of 100 meters of altitude. We defined four altitude zones: foothills (0–700 m), montane (700–1 700 m), subalpine (1 700–2 400 m) and alpine (> 2 400 m). Credits: O. Grente

Let's apply the kernel methodology for each altitude zone, from the one with the highest number of culling events to the lowest. Nevertheless, we excluded from the analysis the alpine zone, to avoid investigation on a too small number of culling events.

► Montane

The kernel Figure 3.48 showed **a reduction of depredation intensity** after the culling events for all spatial distances. Depredations still occurred at high intensity after these events, including right after them, but the periods of time over which they occurred were much shorter than before the culling events. Spots of high depredation intensity at 4-5 km from the events were almost non-existent after the events, suggesting no report of depredation.

Analysed Data

There were 136 unique culling events in the montane zone (700–1 700 m). Their buffers encompassed on average 32 depredations ($sd = 25$) for a total of 4 346 depredations.

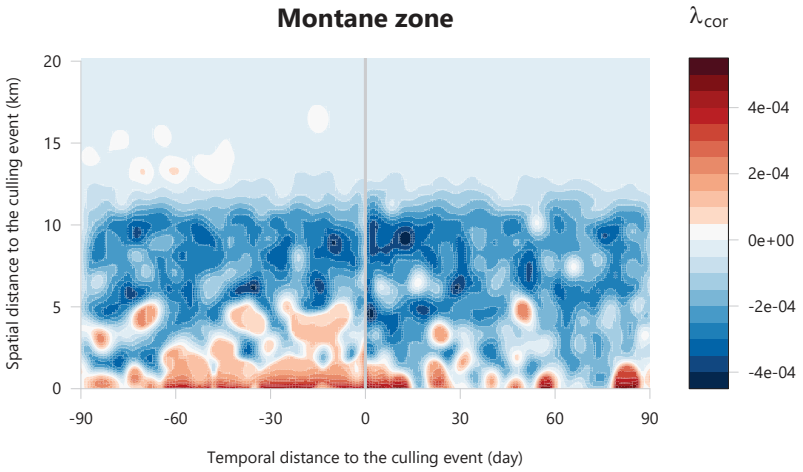


Figure 3.48: Depredation density corrected by pastoral use for the 136 unique culling events of the montane zone. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► Subalpine

The kernel Figure 3.49 showed **no effect of culling events on the depredation intensity** that was almost vertically symmetrical around the culling events line at $x = 0$. Reports of depredation were not suspected either.

Analysed Data

There were 75 unique culling events in the subalpine zone (1 700–2 400 m). Their buffers encompassed on average 38 depredations ($sd = 34$) for a total of 2 902 depredations.

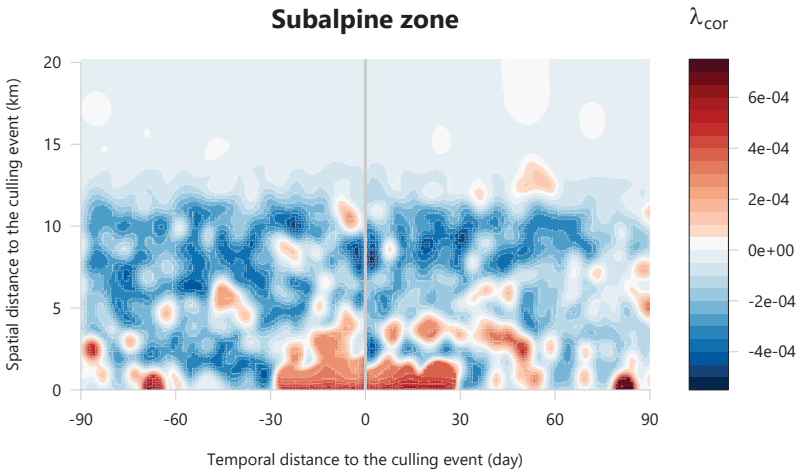


Figure 3.49: Depredation density corrected by pastoral use for the 75 unique culling events of the subalpine zone. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

- **Foothills**

The kernel Figure 3.50 showed **no effect of the culling events on the depredation intensity** too, and no suggestion of a report of depredation.

Analysed Data

There were 19 unique culling events in foothills (0–700 m). Their buffers encompassed on average 19 depredations (sd = 19) for a total of 327 depredations.

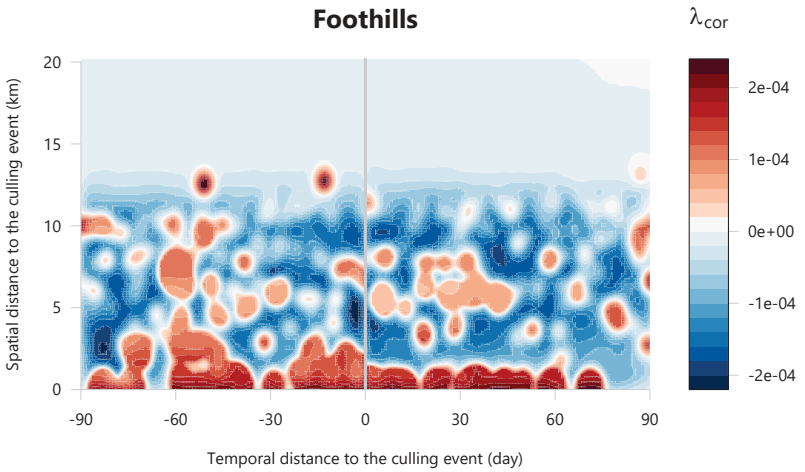


Figure 3.50: Depredation density corrected by pastoral use for the 19 unique culling events in foothills. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

According to the spatial location of culling events...

- the effect of the culling events on depredation varied,
- with a reduction of depredation intensity in:
  - Préalpes de Digne
  - Cerces
  - Trois-Evêchés
  - The montane zone
- with an augmentation of depredation intensity in Vercors
- with an absence of effect in:
  - Mercantour
  - Vanoise
  - The subalpine zone
  - Foothills
- with no clear conclusion on the effects of culling in the massifs
  - Préalpes d'Azur
  - Ecrins 1500
  - Canjuers
- and potential report or spread of depredations due to culling towards close pastures for all massifs except Préalpes d'Azur, Vanoise and Canjuers.

Wolf season

In this section, we investigated the culling effect according to the wolf seasons that were detailed in Chapter 1, Figure 1.2. We used the whole set of 236 unique culling events. The culling events were not evenly distributed amongst wolf seasons (Figure 3.51). Let's apply the kernel methodology for each wolf season.

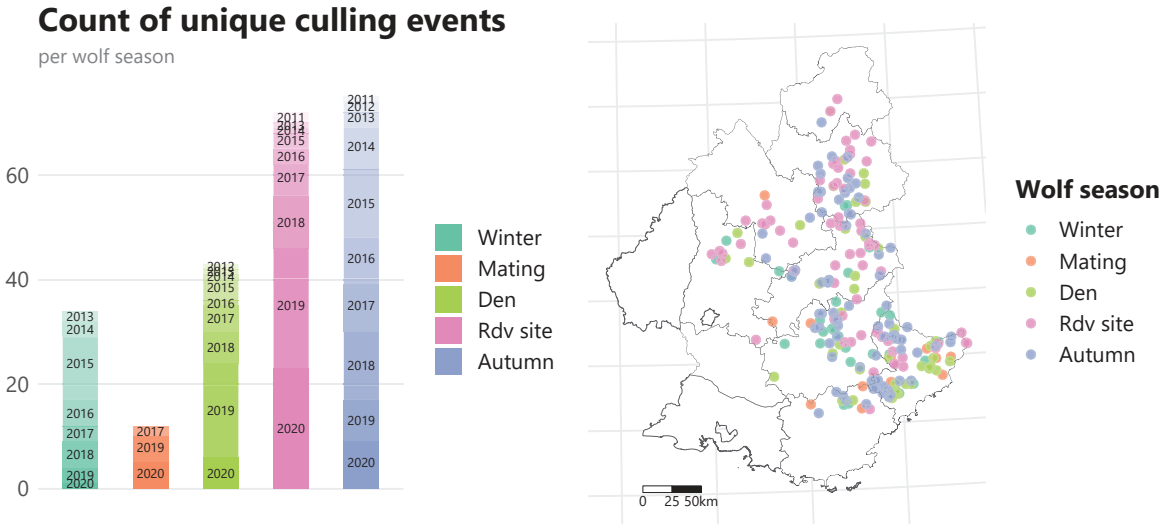


Figure 3.51: Distribution of the 236 unique culling events per wolf season: winter (Nov.–Jan.), mating season (Feb.–Mar.), den season (Apr.–Jun.), *rendez-site* site season (Jul.–Aug.) and autumn (Sep.–Oct.). Credits: O. Grente

► Autumn

Depredation intensity reduced right after the culling events between 1 and 5 km from the culling event locations (*i.e.* dark blue spots), but not between 0–1 km. Positive depredation intensity, predominant between 0 and 5 km before the culling events, became negative after 25 days up to 60 days after these events. Depredation however reappeared with the highest observed intensity at the limit of the study period after the culling events.

Analysed Data

There were 75 unique culling events during autumn (Sep.–Oct.). Their buffers encompassed on average 40 depredations (sd = 33) for a total of 3 035 depredations.

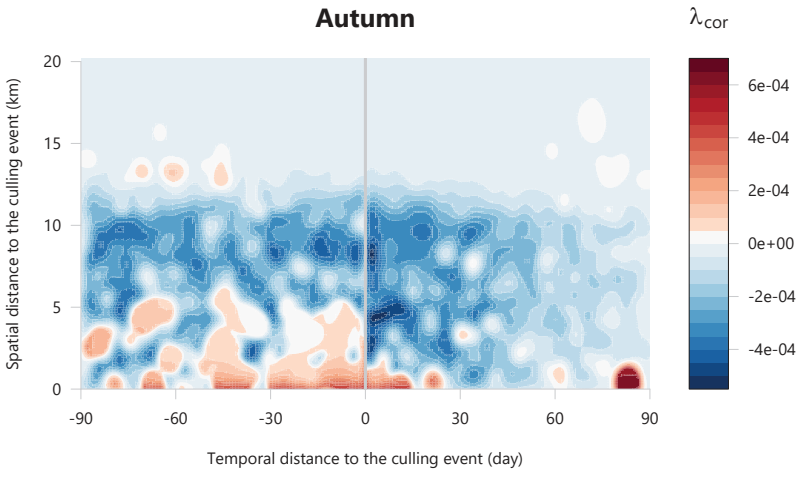


Figure 3.52: Depredation density corrected by pastoral use for the 75 unique culling events during autumn (Sep.–Oct.). Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► ***Rendez-vous* site**

The kernel Figure 3.53 showed **no change of depredation intensity** at the culling event location. However, high depredation intensity appeared after these events up to 6 km, potentially suggesting a spread of depredation due to the culling events.

Analysed Data

There were 72 unique culling events during *rendez-vous* site season (Jul.–Aug.). Their buffers encompassed on average 29 depredations (sd = 26) for a total of 2 068 depredations.

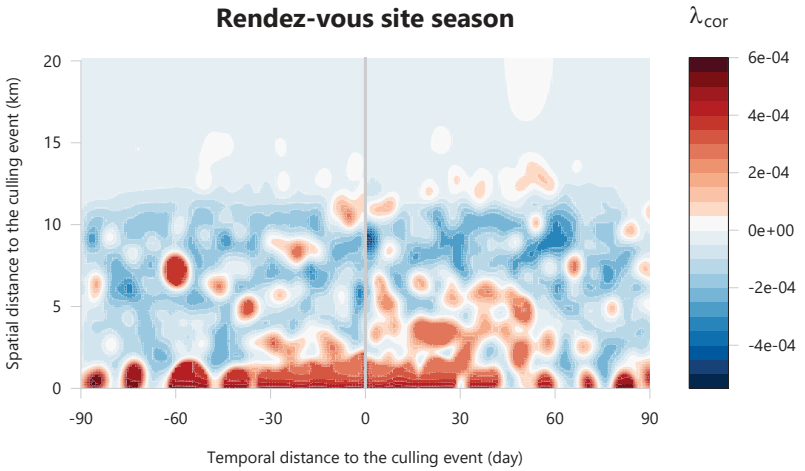


Figure 3.53: Depredation density corrected by pastoral use for the 72 unique culling events during the *rendez-vous* site season (Jul.–Aug.). Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Den site**

The kernel Figure 3.54 showed that the culling events did not prevent the recurrence of depredations after their implementations. The **depredation intensity was even higher after their implementations** compared to before.

Analysed Data

There were 43 unique culling events during den season (Apr.–Jun.). Their buffers encompassed on average 31 depredations (sd = 26) for a total of 1 330 depredations.

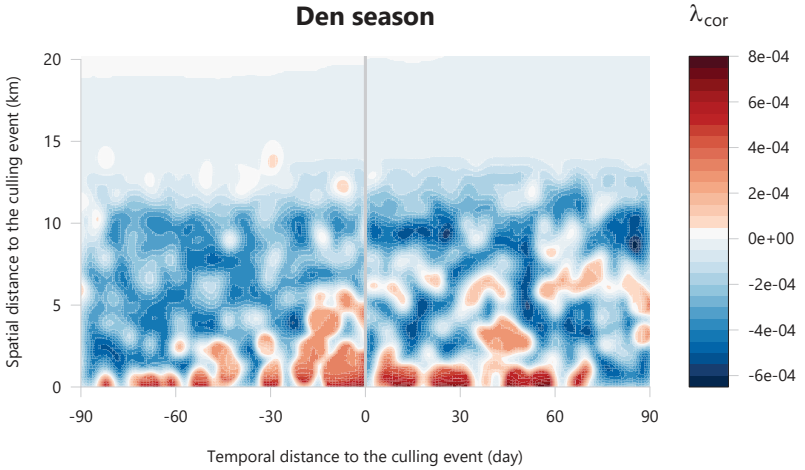


Figure 3.54: Depredation density corrected by pastoral use for the 43 unique culling events during the den season (Apr.–Jun.). Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Winter**

The kernel Figure 3.55 showed that **depredation intensity was higher than expected according to pastoral use after the culling events**, whereas before these events, the difference was less marked. However, after the culling events, these spots of high positive differences occurred over shorter period of times.

Analysed Data

There were 34 unique culling events during winter (Nov.–Jan.). Their buffers encompassed on average 28 depredations (sd = 20) for a total of 953 depredations.

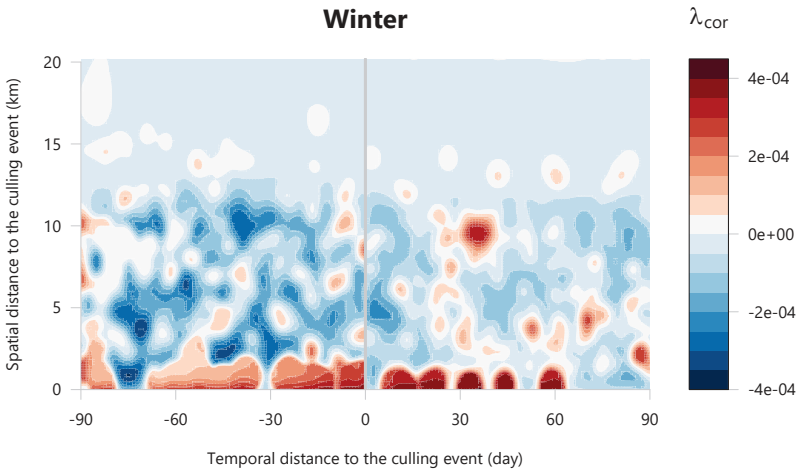


Figure 3.55: Depredation density corrected by pastoral use for the 34 unique culling events during winter (Nov.–Jan.). Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Mating**

The kernel Figure 3.56 showed a situation that worsened right after the culling events and at the location of these events, with depredation intensity increasing after these events. However, except at this area and at this moment, the culling events seemed to induce **an overall reduction in the depredation intensity** for all distances up to 12 km. Depredation mainly reappeared over large spatial distances from 75 days.

Analysed Data

There were 12 unique culling events during the mating season (Feb.–Mar.). Their buffers encompassed on average 30 depredations (sd = 29) for a total of 361 depredations.

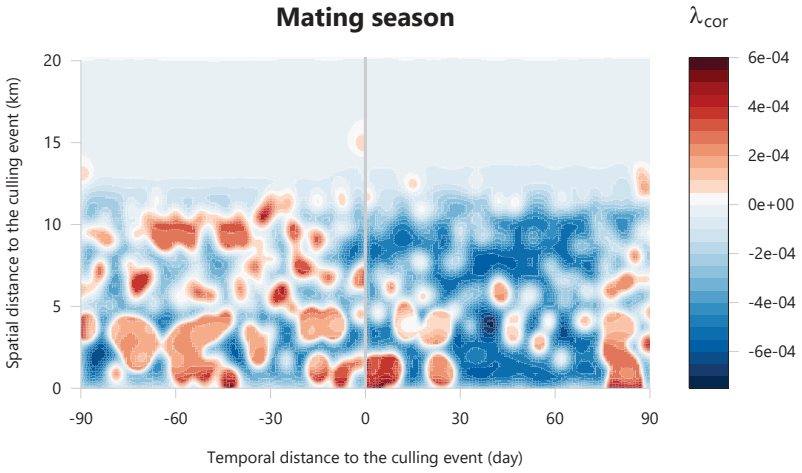


Figure 3.56: Depredation density corrected by pastoral use for the 12 unique culling events during the mating season (Feb.–Mar.). Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

According to the wolf season of culling events...

- the effect of culling events on depredation varied,
- with a reduction of depredation intensity in autumn and during the mating season,

- with an augmentation of depredation intensity in winter and during the den season,
- with an absence of effect in the *rendez-vous* site season,
- with a possible risk of spatial spread of depredation for the culling events in the *rendez-vous* site season.

Culling type

In this section, we investigated the culling effect according to the type of culling: simple defence culling, reinforced defence culling and harvesting. We used the whole set of 236 unique culling events. The culling events were mainly from the reinforced defence culling type with 95 events, the rest being from the simple defence culling type with 78 events and finally from the harvest type with 63 events (Figure 3.57). The harvesting type was more frequent during the first years of culling application.

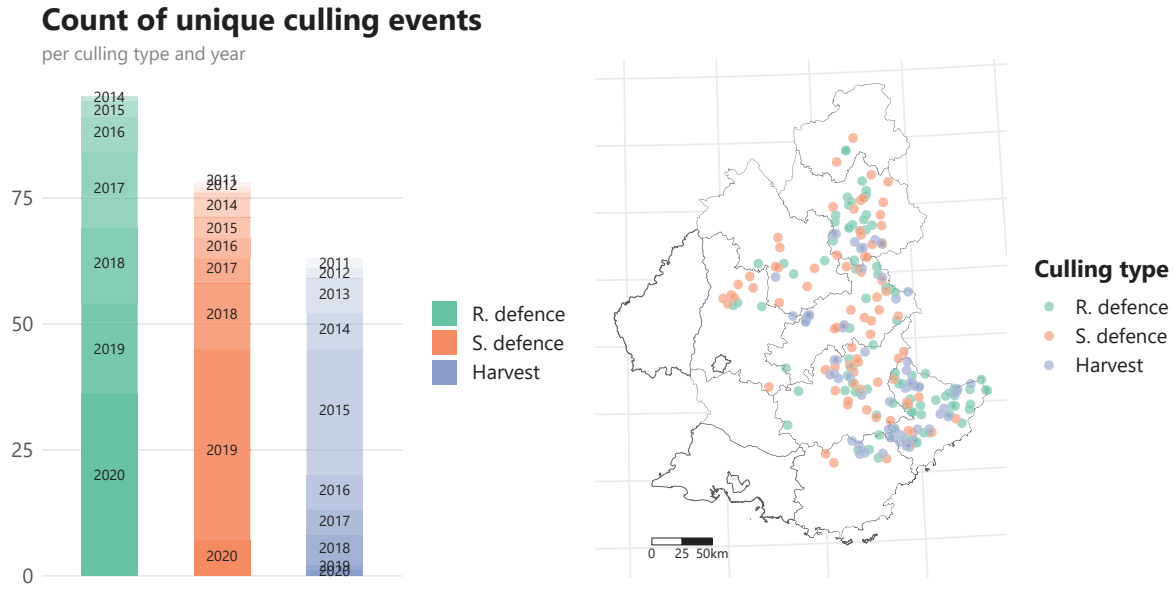


Figure 3.57: Distribution of the 236 unique culling events per culling type, reinforced defence culling type ('*R. defence*'), simple defence culling type ('*S. defence*') and harvesting ('*Harvest*'). Credits: O. Grente

Let's apply the kernel methodology for each culling type, from the most common to the less one.

► Reinforced defence culling

The kernel Figure 3.58 was a figure close to the general kernel figure when pooling all the 236 unique culling events together for the analysis (Figure 3.28). Overall, the figure showed that there was **no change in the depredation intensity before and after the culling events**, for all spatial distances.

Analysed Data

There were 95 unique culling events of the reinforced defence culling type. Their buffers encompassed on average 35 depredations ($sd = 26$) for a total of 3 368 depredations.

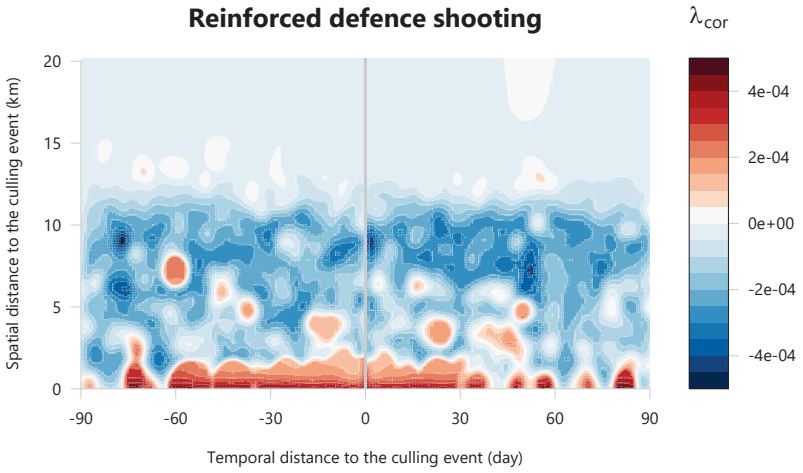


Figure 3.58: Depredation density corrected by pastoral use for the 95 unique culling events of the reinforced defence culling type. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► Simple defence culling

The kernel Figure 3.59 showed that depredation was still present after the culling events, but with higher differences between the observed depredations and those expected according to pastoral use compared to before the culling events. However, the periods of time of these spots of high depredation intensity were shorter and in addition these spots were less spread out over space. **Here, the culling events seemed to allow a reduction of depredation intensity**.

Analysed Data

There were 78 unique culling events of the simple defence culling type. Their buffers encompassed on average 20 depredations ($sd = 18$) for a total of 1 553 depredations.

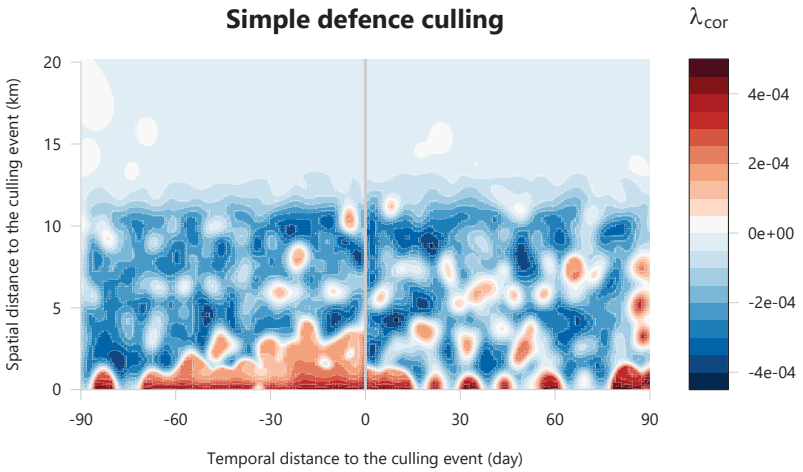


Figure 3.59: Depredation density corrected by pastoral use for the 78 unique culling events of the simple defence culling type. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► Harvesting

The kernel Figure 3.60 showed similar results to those of the defence culling type. Depredation was still present after the culling events, with higher differences between the observed depredations and those expected according to pastoral use compared to before the culling events. However, the spots of high depredation intensity after the culling events occurred on very short period of time compared to the those before the events. In addition, these spots were mainly located at the culling event location, whereas before the culling events these spots could spread up to 5 km. This could suggest that **these culling events reduced the depredation intensity**.

Analysed Data

There were 63 unique culling events of the harvesting type. Their buffers encompassed on average 45 depredations ($sd = 34$) for a total of 2 826 depredations.

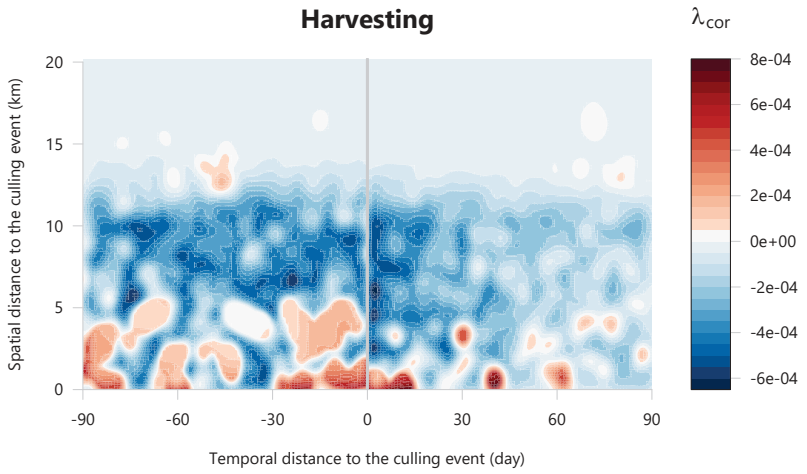


Figure 3.60: Depredation density corrected by pastoral use for the 63 unique culling events of the harvesting type. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

The type of culling event...

seemed to show that reinforced defence culling did not change the depredation intensity whereas the simple defence culling or the harvesting types did, by reducing the depredation intensity. More than an effect of type of culling, this could also reflect different contexts of application, with reinforced defence culling occurring in hotspots, or applied recently in a context of increasing wolf pack density. This will be discussed in the Discussion section.

Culled sex

In this section, we investigated the culling effect according to the sex of the culled wolf. We used the set of 194 unique culling events for which the sex of the culled wolf was known[15]. The events with a removed female or a removed male were almost balanced, with 91 females and 103 males. Females seemed to be more frequently removed in the south of the study area than males (Figure 3.61).

15: For the 42 removals without sex known, this reflected that the culled wolf was deadly hurt but its body could not be found.

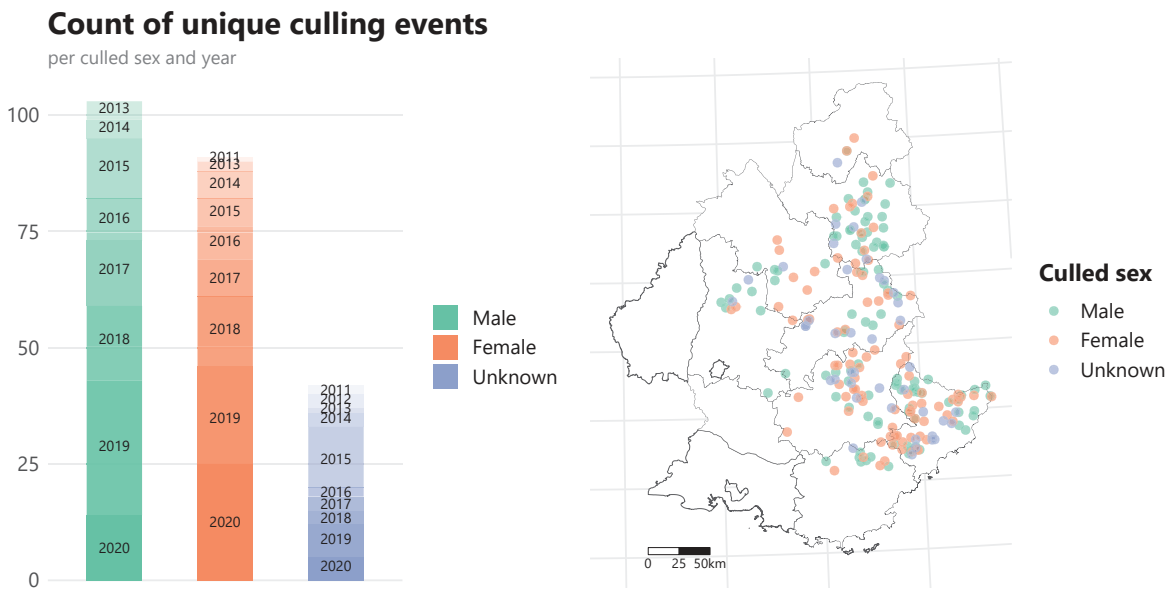


Figure 3.61: Distribution of the 236 unique culling events per culled sex. Credits: O. Grente

Let's apply the kernel methodology on the events that culled males and then on the events that culled females.

► Males

The kernel Figure 3.62 showed that there was **no noticeable change** on the depredation intensity when focusing only on the culling events where a male had been removed.

Analysed Data

There were 103 unique culling events where a male had been removed. Their buffers encompassed on average 34 depredations (sd = 30) for a total of 3 524 depredations.

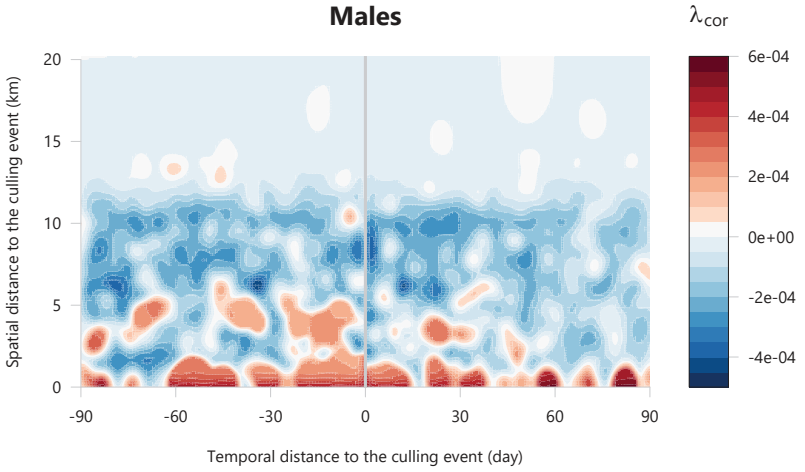


Figure 3.62: Depredation density corrected by pastoral use for the 103 unique culling events of wolf males. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

- **Females**

The kernel Figure 3.63 also showed an absence of change on depredation intensity with the culling of females, at least up to 30 days after the culling events. After this date, the depredation intensity decreased towards the 0 value (white) close to the culling event locations, suggesting that the levels of depredation were expected according to pastoral use in this area. Meanwhile, depredation intensity tended to increase between 30–50 days and between 2–5 km from the events, maybe **suggesting a weak report of depredation**. Before the culling events of females, the depredation intensity was almost systematically above the expected rates according to pastoral use, but only close to the culling events (< 2.5 km).

Analysed Data

There were 91 unique culling events where a female had been removed. Their buffers encompassed on average 32 depredations (sd = 28) for a total of 2 926 depredations.

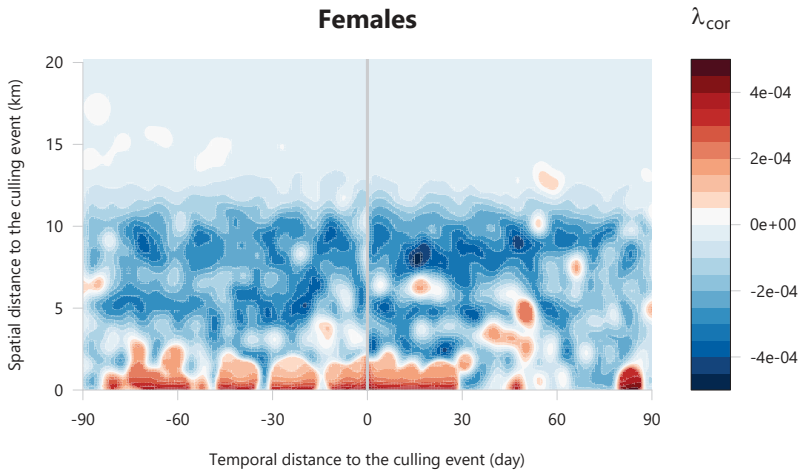


Figure 3.63: Depredation density corrected by pastoral use for the 91 unique culling events of wolf females. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

The analysis of the influence of the sex of culled wolf...

did not allow a clear distinction of effects of culling events according to the culled sex. There was only a potential risk of depredation report for culled females that did not appear for culled males.

The interacting culling events

Up to now, we had only analysed the 236 unique culling events, *i.e.* the culling of one wolf separated from the other culling events by at least 5 km and 25 days. There were 111 culling events that did not fit this definition: we called them the **interacting culling events**. There were two classes of interacting culling events:

- The **interacting simultaneous culling event**: it corresponded to one culling event occurring simultaneously to another culling event (*i.e.* which was separated by exactly 0 km and 0 day from another culling event).
  - There were 52 culling events of this type.
  - 56% were defence culling, 44% were harvesting.
- The **interacting non-simultaneous culling event**: it corresponded to a culling event which was separated by less than 5 km and 25 days from another culling event, but by more than 0 km and 0 day.

- There were 59 culling events of this type.
- 92% were defence culling, 8% were harvesting.

The interacting culling events were more frequently encountered in the south of the study area and in the last years of the study period (Figure 3.64).

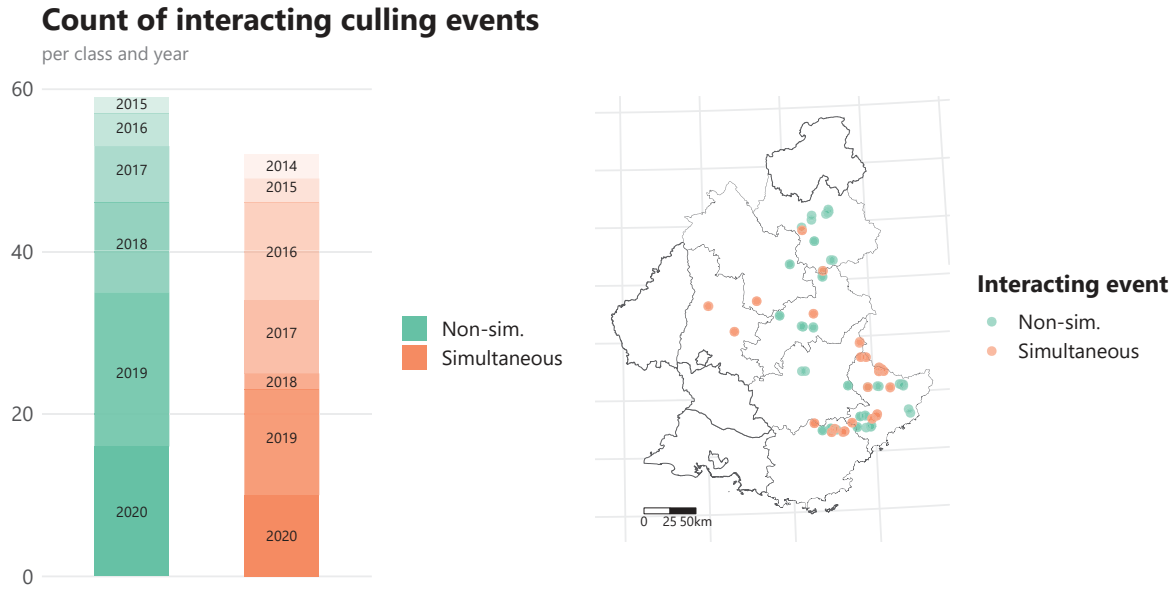


Figure 3.64: Distribution of the 111 interacting culling events per class and year. Credits: O. Grente

We needed to slightly adapt our methodology previously used for unique culling events. The reason for this was that the depredation intensity of one buffer of an interacting culling event could be influenced by the depredation intensity of another buffer. If we did not adapt our methodology, the depredation intensity for example before one of these events, at time < 0 in the kernel figure, could in fact already be affected by another culling event occurring beforehand.

Therefore we pooled the interacting events into groups. One group corresponded to a set of interacting culling events separated from each other by less than 5 km or 25 days (regardless if they were simultaneous or not). Note that:

- There could be mixed groups, with non-simultaneous and simultaneous culling events in the same group.
- For the special case where two culling events A and C were not interacting, but were both interacting with event B: we considered A, B and C were part of the same group of interacting culling events.

There was a total of **50 analysed groups**. One group corresponded to the death of on average 2.22 wolves ($sd = 0.51$).

Then, we determined the buffer for each group:

- The spatial buffer corresponded to the pastoral surfaces overlapping, totally or partially, with the circle of 10-km radius centred on the centroid of the culling events of the group.

- The temporal buffer corresponded to the following period:
  - 90 days before the date of the first culling event of the group
  - 90 days after the date of the last culling event of the group

This meant that all the depredation events occurring between the first date and the last date of the group were not part of the analysis. **The analysis therefore compared the depredation intensities before the first culling event of a group of interacting events, to the depredation intensities after the last event of this group**. Note that for groups only constituted by simultaneous culling events occurring during the same attack, the events all had the same location and date: therefore, the methodology applied was exactly the same as for the unique culling events.

Then, the same kernel methodology could be applied[16]. We separated the analysis for *1)* the groups which were only constituted by interacting simultaneous culling events and *2)* the groups which were only constituted by interacting non-simultaneous culling events. There was 5 mixed groups (*i.e.* groups with both classes of multiple events) that we pooled with the first group, because the number of simultaneous deaths exceeded the one of non-simultaneous deaths.

16: Note that we applied again the rescaling of the depredation intensities of the pastoral correction according to the range of the observed intensities (corrected for outliers). We already applied this rescaling when exploring the variability of the unique culling events in section *Variability of the culling effects*.

- **Interacting and simultaneous**

The kernel Figure 3.65 showed a **clear reduction of depredation intensity** right after the groups of simultaneous culling events, at the proximity of the centroids of these groups, up to the end of the study period. However, high depredation intensity appeared at 45 days between 2–5 km. Before the events, depredation was not as intense between 2–5 km. This could suggest a **depredation report** at these distances.

Analysed Data

There were 52 interacting simultaneous culling events pooled into 24 groups (including 5 mixed group each including 1 non-simultaneous culling event). The group buffers encompassed on average 47 depredations (sd = 28) for a total of 1 139 depredations.

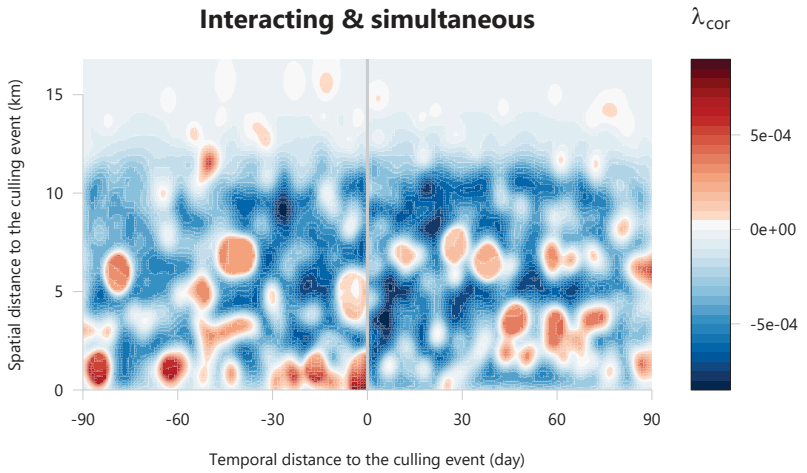


Figure 3.65: Depredation density corrected by pastoral use for the 24 groups of interacting simultaneous culling events. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

► **Interacting and non-simultaneous**

The kernel Figure 3.66 showed a weaker **effect** of the interacting and non-simultaneous culling events compared to the simultaneous events. Depredations were still present after these events. They were nonetheless more spread out in space before the events compared to after.

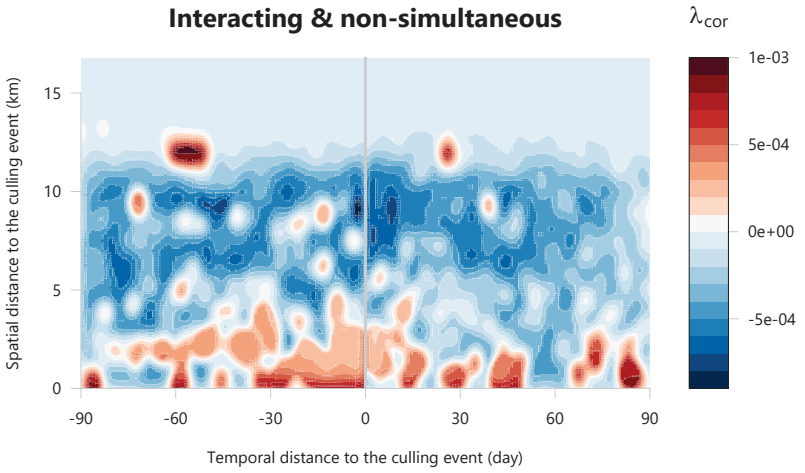


Figure 3.66: Depredation density corrected by pastoral use for the 26 groups of interacting non-simultaneous culling events. Higher values than 0 indicated that the observed depredation density was higher than the one expected according to the pastoral use. Credits: O. Grente

Analysed Data

There were 54 interacting culling events that involved non-simultaneous deaths of wolves, pooled into 26 groups. The group buffers encompassed on average 39 depredations (sd = 23) for a total of 1 014 depredations.

The analysis of the interacting culling events...

- Required to adjust the previous methodology,
- By pooling the events that were interacting into unique groups,
- And by applying the kernel method on these groups,
- and showed that the deaths of wolves during the same culling event could be more efficient to reduce depredation intensity than the deaths of wolves close in space and time but during two different culling events.

Operations of *brigadiers*

In this final section of analysis, I investigated the database of operations of brigadiers, described in section *Operations of brigadiers*. These operations were mainly located in the south of the study area, where were located the hotspots of depredation (Figure 3.13). Reports of operations were only available for the most recent years of the study period, from 2016 to 2020.

An operation was generally constituted by several days of watching. An operation had therefore a similar structure than a group of interacting culling events occurring over several days. Therefore, the methodology developed just before for the interacting culling events was applied for the operations of brigadiers. **The analysis therefore compared the depredation intensities before the beginning of an operation, to the depredation intensities after the end of this operation**.

All operations did not result in the death of a wolf. In fact, most of the 145 available operations ended in no observation of a wolf (46%). For 26% of operations, one wolf at least was seen, but without shooting fired

(*e.g.* the wolf was not interested by the flock or because of bad weather). For 13% of operations, the attempts of shooting were all missed. Finally, for the last 15% of operations, at least one shoot was successful and killed a wolf.

I investigated the effects on depredation that the operations of brigadiers could have, by pooling the operations according to their results. I did not analyse the operations without wolf observed. Results are displayed in appendices, section *Complement for results on operations* on page 303. Operations without shot or with a successful shot did not provide results with noticeable effects on depredation intensity, which remained high at proximity of the operation locations, whether it was before and after the operations (Figure C.5, Figure C.7).

There was however only an interesting signal regarding the operations with missed shot (Figure C.6). Depredation intensity seemed to spread out over space after these operations. I took advantage of the fact that operations provided more information than the culling events. I divided the operations with missed shot according to the fact that brigadiers observed one single wolf, or that at least two wolves were simultaneously approaching or attacking flocks as a group. Results are provided below[17]. However, **the number of operations for each group was extremely low, therefore we should not put too much weight on these results**.

17: Note that I also applied the same analysis to the operations with successful shot or those without shot, but the results did not produce noticeable effects on depredation intensity. Results are not shown.

- **Missed shot, single wolf**

Analysed Data

There were 13 operations with only missed shots where only wolves alone were seen. The buffers of these operations encompassed on average 45 depredations (sd = 29) for a total of 580 depredations.

The kernel Figure 3.67 showed that missed shots did not result in the reduction of depredation intensity. Nevertheless, spots of high depredation were less spread out over space after the missed shots at immediate proximity of the operation locations (between 0–5 km). However, high depredation intensity spots appeared right after the operations between 6–9 km during 20 days after the operations, along with spots from 50 days between 3–6 km or at 11 km from the operations. This could suggest a **spread of depredations in space**.

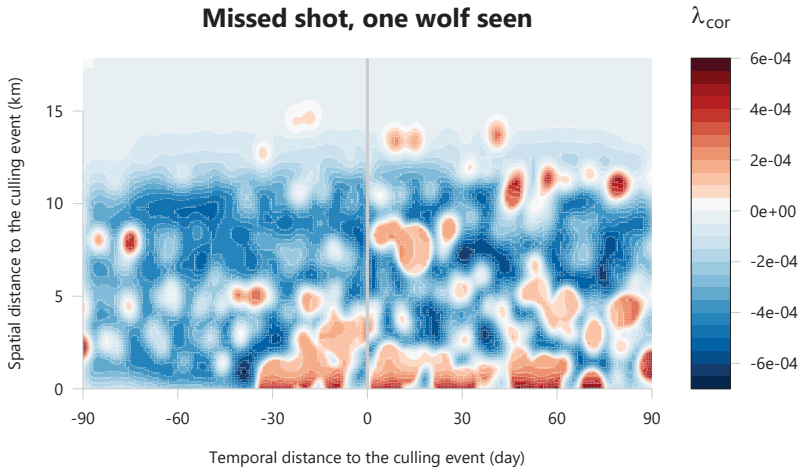


Figure 3.67: Depredation density corrected by pastoral use for the 13 operations with only missed shots and observations of single wolves. Credits: O. Grente

► **Missed shot, group of wolves**

The kernel Figure 3.68 almost showed the opposite results compared to Figure 3.67. Here, the missed shots seemed to have a beneficial effect, as right after the operations, the depredation intensity, especially between 0–5 km from the operations, was mostly negative. Only one spot of very high depredation intensity was present after the operations, between 50–60 days.

Analysed Data

There were 6 operations with only missed shots where several wolves were seen. The buffers of these operations encompassed on average 61 depredations (sd = 36) for a total of 366 depredations.

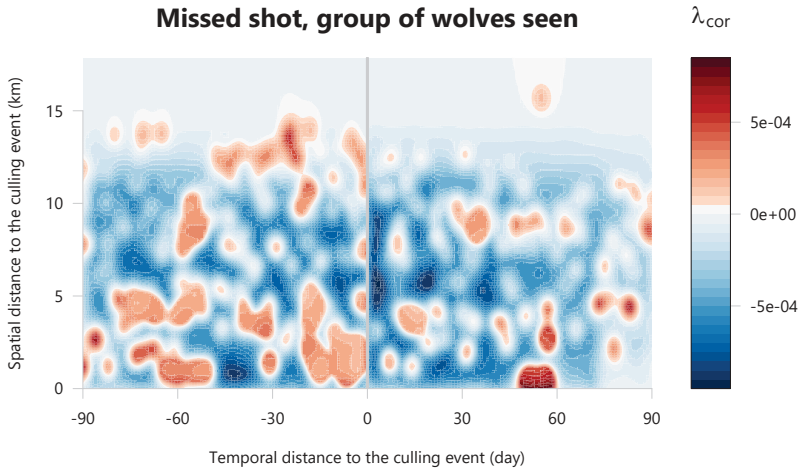


Figure 3.68: Depredation density corrected by pastoral use for the 6 operations with only missed shots and observations of groups of wolves. Credits: O. Grente

I also investigated other variables related to the operations.I searched to analyse the operations according to their lengths (in days), to their number of teams (from 1 to 3), to their locations (in massifs), to the presence or absence of guarding dogs and fences (combined or not) or to the number of days for which at least one wolf was seen. The analysis was however inconclusive for two reasons:

1. It was necessary to divide the operations according to their result (successful shot, missed shot, no shot, no wolf seen). The number of operations was 145, therefore the division created small operations groups, especially because the group without wolf seen represented almost half of the dataset.
2. To this, was added **a lack of variability** for most of the investigated variables[18].

Consequently, it was frequent to obtain groups with less than 5 operations for some categories, weakening too much the kernel analysis.

The analysis of the operations of *brigadiers*...

- Required to use the same adjusted methodology as the interacting culling events,
- Did not show an effect of operations according to their result,
- Was not possible when investigating other variables, as flock protection, because of a lack of variability,
- But provided an interesting result regarding the differences between operations with lone wolves seen or with groups of wolves seen, however only for operations with missed shots. They represented very small groups, weakening the analysis.

18: As seen in Figure 3.13, most operations occurred in the four massifs all in the south of the study area. There were only 9% of operations where flocks were not protected (by dogs and/or fences). Operations could last from 1 to 5 days, but there were 43% of operations lasting 4 days (because *brigadiers* were generally deployed from Monday to Thursday in the same pasture). Therefore, some groups of operations were under-represented and others over-represented.

3.5 Discussion

The choice of the developed method

The study design

The available data were retrospective, in short they were not part of a scientific study. This prevented us to use the most robust study design, which is the experimental design. This left us with three possibilities: correlation, *inter-site* comparison and *intra-site* comparison. Correlation was the less robust study design, so we decided not to adopt this approach. We preferred the *intra-site* comparison over the *inter-site* comparison. We thought that it was less risky to compare the same pastures across time, than to compare different pastures according to if they used lethal removals or not.

We could have combined both *intra-site* comparison and *inter-site* comparison, as recommended by [246], to transform the *before-after* study design into a Before-After-Control-Impact study design (BACI) that the author considered more robust. In BACI study design, before-after comparisons are themselves compared between controls (areas without culling for example) and treatments (areas with culling).

[246]: Khorozyan (2021), 'Defining Practical and Robust Study Designs for Interventions Targeted at Terrestrial Mammalian Predators'

Actually, we did perform BACI in section 12 (Method 3: estimated seasonal dynamic without culling) on page 166, when we computed the 'non-culling events' which could be assimilated to controls. However, I was not convinced by this method, mainly because I considered that the variability between culling events and non-culling events was too high. Not only the pastures may not be identical in many ways, for the pastures using culling and also for the pastures adjacent to them. In addition, the whole situation surrounding these pastures may be very different even if the pastures are not far from each other: the *rendez-vous* site may be located differently compared to flocks, the pastures may be separated by a valley, the forest cover may not be identical *etc*...

This variability was extremely visible when we investigated the culling effects according to various variables, for example the massif location. To sum up, it was already difficult to draw a unique and general tendency when comparing the situation before and after the whole set of culling events. To me, it seemed impracticable to add on top of this a double comparison with non-culling events. This was the reason why I decided to focus on the pastoral correction rather than using BACI through non-culling events. The pastoral correction was absolutely not a way to remove the entire risk for confounding factors, but it removed (with limited efficiency) the most important confounding factor, namely the spatio-temporal use of pastures by flocks.

The most closest method previously used was the method from [248]. We improved her method by making the use of space and time explicit, where she had used discrete spatial and temporal classes. In addition, we used a different approach to correct for the use of pastures by flocks. We directly used the information provided by a pastoral census, which detailed the use by sheep flocks for each pasture. We considered this approach as the most precise approach ever used in a study using retrospective data about the lethal removals of canids.

[248]: Le Cam (2012), *Evaluation de l'efficacité de la mise en place de tirs de défense ou de prélèvement sur les attaques des troupeaux domestiques par le loup Canis lupus*

The kernel method

Once you choose a study design and *what* to compare, you then have to choose *how* to do the comparison. For example, [248] used the statistical z-test to compare the mean of the depredation count (corrected by pastoral use) between two periods of time, for a fixed spatial class, before and after the authorisation decree. This test provided a convenient *p-value*, taken as a statistical and objective proof of 'validation' that the observed differences in the mean of depredation counts, if any, were due to the decrees.

Here, we chose to stop the analysis to the kernel estimation of depredation intensity. **We did not include any summary metric** (for example the differences between the mean of the depredation intensity before and after the culling events), **and we did not use a statistical test to evaluate the statistical validity of such metric**. This could appear surprising considering that almost all if not all studies that I mentioned in the literature review used statistical tests.

We made this choice against the flow for various reasons, that could be summed up in one sentence: keep the results simple and complex at the same time. Let me explain this sentence in more thorough details.

- **Keep the results simple...**

We could have used statistical tests in addition to the kernel analysis. It could have been two complementary approaches. However, there were many results to show, because it was essential to present the variability of the effects of culling. I could not only provide the general result for the whole set of 236 unique culling events. Even if I restricted the results of variability to the massifs, there were still 9 different results to show. Given that, to fully understand the figures, one has to go through the whole methodology first. The multiplication of results would have been a too high risk of confusing people. Therefore, I decided to keep the results **as simple as possible**. Consequently, I had the choice: providing the kernel results or statistical results, but not both. You already know I decided the first option.

The use of statistical tests as [248] did, would have required to use fixed spatial and temporal classes. For example, it would have required to compare the depredation level from a specific class of time (let's say from -20 to -10 days) and from a specific class of spatial distance (let's say between 0–1 km) to another specific period of time and spatial class. Now, imagine you want to test all possible combinations of temporal and spatial classes. Let's use the same classes as in the kernel analysis: 500 meters and 2 days, for an analysis over 10 km and 90 days before and 90 days after the culling events. There would be $45 \times 20 \times 90 = 81000$ combinations (45 temporal classes before or after the culling events, 20 spatial classes, 90 total temporal classes).

On the other side, the kernel figures had the advantage of summarising the whole depredation process around the culling events. One look at the kernel figures and you could know the overall effect of the analysed culling events between 0–10 km, from 90 days before the events, to 90 days after. Going through a large table of *p-values* would have been a much overwhelming information, or in the case where I would have used

fixed spatial distances as [248], it would have led to a loss of results as explained earlier. Moreover, I believe in the strength of visual results for communication, especially when considering that a non-scientific public could be interested by these results.

- **...and complex at the same time.**

You could argue that there was no need to test all combinations, and simplifications could have been used. This was what [248] did: she compared the temporal classes for the same fixed spatial class. She also increased the size of classes: she used a 2-km class and a 7-day class or larger. However, I believe the strength of our analysis was the continuous use of space and time. Fixing classes, or analysing over large classes, would have decreased the quality of our results because we would have lost this strength and the details of our results. In short, this would have led to an **oversimplification of the interactions between depredation and culling**. For example, in both cases, it would have made the observation of potential depredation reports or spreads impossible. Eventually, the risk for using a *p-value* was to simplify the effects of culling to a 'yes' or a 'no' answer, where the interactions between both culling and depredations were much more complex, especially because they were taking place in a 3D space.

It may seem heretical but I also do not believe that the statistical significance is the only possible answer when studying ecology. First, the *p-value* can lead to wrong interpretations. They can be made by the scientists themselves [263]. For example, [248] concluded that a non-significant difference in the depredation counts before and after the decrees meant that depredations were '*stable*'. This was not correct because a non-significant difference only showed an absence of proof of changes induced by decrees, instead of a proof of absence of changes. A peer-review of her work would maybe have made her correct this wrong interpretation. However, even if the article was corrected, it is even harder for managers or the public to understand why a non-significant result does not necessarily indicate an absence of effect.

[263]: Amrhein et al. (2019), 'Scientists Rise up against Statistical Significance'

Moreover, a statistical result generally implies for the public that it is an objective and reliable result because it is mathematical [244]. Because of this, there is generally too much weight put on significant statistical results, seen as the absolute truth. However, as [264] wrote, '*the P value [...] is neither as reliable nor as objective as most scientists assume.*'. The risk that an error crept into the methodology, turning the results into wrong *p-values*, is existent. Moreover and more importantly, I believe **a non-significant statistical result could be ecologically or socially significant, and at the same time, a statistically significant result could be ecologically or socially non-significant**. Therefore, I found difficult to summarise the culling effects through the use of a *p-value*.

[244]: O'Neil (2016), *Weapons of Math Destruction: How Big Data Increases Inequality and Threatens Democracy*

[264]: Nuzzo (2014), 'Scientific Method: Statistical Errors'

In short, I believe that the kernel method was the **good compromise between simplification and complexity**: it allowed a fast and efficient communication about the effects of culling events, without erasing the spatial and temporal complexity of the process.

Interpretation of our results

Combining all culling events we had at our disposal in the same analysis provided a homogeneous pattern of depredations, where no effect of culling emerged. When dividing the analysis according to the characteristics of culling events, such as the season of the culling events, effects could emerge for certain groups. These effects could be varied. Some groups of culling events seemed to induce a decrease of depredation levels, others an increase, both types could be combined or not with a spatial report or spread of depredation to adjacent pastures (from 3–10 km, mostly around 5 km). **Be careful: the depredation levels mentioned are those corrected by pastoral use.** Therefore, these levels are not the raw count of depredations, but the differences between the observed level of depredation and the expected one according to pastoral use. As in the previous sections, I will use 'depredation' for ease of reading.

Are reinforced defence less efficient?

Therefore, the general analysis was concealing the effects of culling events depending on their contexts. This could explain why there was no effect of culling when applied in the context of reinforced defence, whereas the simple defence or harvesting were reducing the depredation levels. The reinforced culling was the group of culling type with the highest number of culling events (95) although it was not so much higher than the simple defence (78).

However, there were two biases in the applications of the types of culling that could also explain the lack of effect of reinforced defence, this lack seeming counter-intuitive given the results of simple defence. Because there is a limited number *brigadiers* and *lieutenants de louveterie*, their operations (*i.e.* reinforced defence) were mostly directed by prefects in hotspots of depredation, whereas in practice, simple defence could be applied at any time if the livestock owner had subscribed to subventions for protection measures and implemented these measures.

The second bias was related to time. Culled wolves in the context of reinforced defence started in 2014, and reinforced defence was mostly represented in the last years of the study period (from 2017 to 2020), while it was the opposite for harvest, being the predominant culling type to kill wolves from 2011 to 2015. The wolf population number but also the pack number and therefore density had increased within France by following an exponential growth, with a total of 19 observed packs in 2011 compared to 106 packs in 2020. Almost all these packs were or are in the French Alpine Arc.

Consequently,we could not expect the same efficiency in reducing depredation from reinforced defence as in the simple defence where the level of depredation before the intervention was lower, or as in harvesting where wolf and pack densities were lower. This is a good example that, when comparing effects between groups of culling events, one has to compare the baseline situation regarding depredation before the culling events, but also the more general spatio-temporal context of these groups.

The spatio-temporal contexts

The most striking effect concerned the results for **massifs**. In Préalpes de Digne, Cerces and Trois-Evêchés the culling events seemed to have a brutal reducing effect on the depredation levels, whereas in Vercors, the results could suggest an increase of depredation intensity due to culling. These differences could be linked to the different natural environments in these massifs, themselves causing different pastoral practices.

This could also be linked to the colonisation process of grey wolves. With Vanoise, Vercors is the only massif isolated from the others by a highway. Vercors is also located along the metropolis of Grenoble (445 059 inhabitants in 2018, source INSEE), the highest metropolis inserted within the analysed massifs[19]. This could suggest a different dynamic of the wolf population in Vercors. This could also be linked to the fact that depredations were spread in space and time always at high intensity before the culling events, especially compared to the massifs where culling was associated to a reduction (*e.g.* Préalpes de Digne, Trois-Evêchés).

19: In comparison, two other metropoles inserted within the analysed massifs, Gap and Dignes-les-Bains, had 50 302 and 16 333 inhabitants in 2018 (source INSEE).

The investigation of the culling effect by **altitude** did not provide contrasted results, suggesting that the variability in culling effects due to locations was better explained by massifs. The classes of altitude we used could also be too large.

The results according to the **wolf season** were also contrasted, with the den and winter seasons associated with a potential increase of depredation after the culling events, whereas the autumn and mating seasons were associated with a potential decrease of depredation after the culling events. None of these four seasons were associated with report or spread of depredations contrary to the *rendez-vous* site period. Without more investigation at the finer scale, it is difficult to interpret these results. I will nonetheless attempt an interpretation, mostly based on what I developed during the first and second chapter of the thesis, but we should remain cautious.

1. *Autumn (Sep.–Oct.)*

The additional deaths due to the culling events between September and October could have decreased the size of packs which was generally at its highest in the year[20]. This would in turn decrease the needs for dispersal. This could have then balanced pack food needs. The decrease in depredation observed for this group of culling events could then suggest that the reduction in food needs was higher than the reduction in dispersal needs.

20: See for example this blog post from the OFB: A pack of 13 wolves, is that surprising?

2. *Winter (Nov.–Jan.)*

In winter, packs are generally smaller due to autumn dispersal, and the risk for pack dissolution is higher for smaller packs [174]. However, if culling was causing dissolution, we should see a decrease of depredationj at the location of the culling and an increase elsewhere, whereas we observe an increase at the culling location. This increase could maybe be due to a perturbation in the breeding pairs: if a breeder was killed, this could have opened doors for subordinates to reproduce, maybe leading to multiple reproduction within the same pack [178].

[174]: Brainerd et al. (2008), 'The Effects of Breeder Loss on Wolves'

[178]: Ausband et al. (2017), 'Effects of Breeder Turnover and Harvest on Group Composition and Recruitment in a Social Carnivore'

3. *Mating season (Feb.–Mar.)*

This interpretation could appear contradictory with the decrease detected during the *mating season*. Indeed, the loss of a breeder during the mating season should also lead to higher risks for multiple reproduction. However, maybe the loss of a breeder during the mating season occurred too lately to be rapidly replaced by a subordinate or a disperser; this could have decreased the chance for successful reproduction, and could in turn have decreased the food needs within the territory.

4. *Den season (Apr.–Jun.)*

When pups are born, the food needs increase. The loss of a subordinate or a breeder induced by culling in the den season should decrease pup survival [265], and so food needs. The increase after culling and at the culling location, without report of depredation, for culling during the den season suggested that the risks for pack dissolution was low. Maybe this could suggest that a breeder loss at this time could also have caused multiple reproduction, as in winter. But it was not consistent with the interpretations from the mating season. This reminds me the preamble of Chapter 1, where a breeding female was culled during autumn in the exact same area of Mercantour-Argenterra where another breeding female had already been culled at the beginning of July.

[265]: Ausband et al. (2017), 'Harvest and Group Effects on Pup Survival in a Cooperative Breeder'

5. *Rendez-vous site season (Jul.–Aug.)*

Culling individuals during this period should have decreased pack size but also the needs for dispersal, therefore balancing the food needs. This could then explain the absence of effects of culling events during this period. However, this was not consistent with the suspected spread of depredation around 5 km occurring right after the culling events. This spread could be due to dispersal from the concerned territories or from adjacent wolf territories, however this would suggest that this dispersal would have occurred in September or before, which seemed too soon considering the wolf life cycle. If this spread was caused by pack dissolution, there should be a reduction of depredation at the culling location (*i.e.* it should be a report and not a spread), whereas it was not observed in our results.

If you have to remember one thing from our study

The main message of this study is that **a general and unique effect of culling events is highly unlikely in the French Alpine Arc**. Culling events were all associated with different contexts, whether it was due to the immediate environment or the season, that could have induced different situations for flocks, wolves, wild prey or humans. Therefore, pooling all culling events together only provided a blurred result where no effects emerged, whereas these effects emerged when dividing the analysis by groups of culling events according to their characteristics. Ideally, we would have combined the location and season to pool culling events. However, the number of culling events was limited, and multiplying the number of combined groups would have resulted in too small groups and a drop in the confidence of our results.

The differences with North America

Different contexts

In addition to pastoral practices[21], there were two main parameters explaining why the situation in France was very different to the situations in North America: the wolf density of the removal intensity. It is of paramount importance to describe these differences before doing any attempt of comparison between our results and results in studies focusing on North America.

21: mentioned in Introduction, section *Different contexts of depredation*

1. *The wolf density*

The first parameter was related to the wolf density. For example, the study of [52] analysed the effect of culling for Michigan (250 941 km^2) where the highest annual abundance of wolves was reported at 70. In [96], there were a maximum of 1 645 wolves at the end of the study period in the three wolf recovery areas (~ 734 000 km^2), being 2.2 wolves/100 km^2. In the French Alpine Arc, 624 wolves were estimated at the end of 2020, essentially located within the French Alpine Arc (62 527 km^2), being 10 wolves/100 km^2.

[52]: Santiago-Avila et al. (2018), 'Killing Wolves to Prevent Predation on Livestock May Protect One Farm but Harm Neighbors'

[96]: Bradley et al. (2015), 'Effects of Wolf Removal on Livestock Depredation Recurrence and Wolf Recovery in Montana, Idaho, and Wyoming'

In the French Alpine Arc, the area seemed quite saturated in wolf packs [29], and the wolf population in France was constrained to this region, with only a few reproductive packs known outside of the region (only one existing reproductive pack in 2020, located in Jura). In the USA, the wolf population do not seem to be constrained to mountains, maybe because human density is weaker in these States than in France. As we have seen in the literature review of Chapter 1, a difference of wolf density can greatly modify the dynamic of a wolf population. In saturated populations, packs tend to become larger and the proximity between packs is also higher. Therefore, this could accelerate the replacement of lost breeders and decrease the risks of pack dissolution.

[29]: Réseau Loup-Lynx (2021), *Bilan de suivi hivernal de la population de loups - Hiver 2020/2021*

2. *The removal intensity*

In the USA, the intensity of lethal removals was generally higher than what was applied in France. In [96], entire wolf packs were removed by aerial shooting. Their lowest intensity of removals, called '*partial removal*', removed 2.2 wolves on average per intervention. This corresponded to the number of wolves culled in France per group of interacting culling event (on average 2.2 wolves, $sd = 0.51$). When adding the 236 unique culling events, the mean of wolf killed per intervention dropped to 1.1 ($sd = 0.33$). In France, there was no pack removal, and there was no aerial shooting. If we compare to coyote interventions in the USA, the same applies (*e.g.* 4.9 culled coyotes per aerial intervention in [253]).

[253]: Wagner et al. (1999), 'Effect of Preventive Coyote Hunting on Sheep Losses to Coyote Predation'

In the USA, each depredation can be followed by a lethal intervention regardless of the recurrence, whereas in France, the most efficient removals (reinforced defence and harvest) were authorised only above a certain level of depredations. Consequently, the ratio of the number of depredations on the number of culled wolves was generally much higher in the USA compared to the one in France. In our study, we analysed 7 747 depredations for 236 unique culling events, therefore a ratio of 33 depredations per culled wolf. In [97], there was 525 culled wolves for 923 total depredations in Minnesota (for a study period of 20 years),

[97]: Harper et al. (2008), 'Effectiveness of Lethal, Directed Wolf-Depredation Control in Minnesota'

being a ratio of 1.76 depredation per culled wolf. This situation also partly explains why the approaches used by studies focusing on the American situation differed from ours. They studied the presence or absence of depredation (through depredation recurrence rate [52, 96, 97]) because their amount of analysed depredation and culling events were in the same order of magnitude. In our case, we could extend the study from presence/absence to depredation density because the amount of depredations in France largely exceeded the amount of culling events.

Contrasted results

Now that we have established the differences between the American and the French context, let's attempt a comparison between the results from studies focusing in America and from our study.

Brief summary of findings in North America

What has been shown in the North America for the effect of wolf culling on depredation is a weak reduction of depredation risk at the removal location after the removals of a few wolves [96, 97, 99]. This turned into a strong depredation reduction when packs concerned by depredations were removed ([96]) or the majority of wolves in the area were removed [99]. In the case of pack removal, the delay before next depredation had a median of 730 days (contrary to 64 days for the partial removals of on average 2.2 wolves, and 19 days for no removal) [96]. However, [52] showed a potential risk for report of depredation that was not statistically confirmed: '*insignificant 22% increase in risk of recurrence at sites up to 5.42 km distant in the same year, compared to the non-lethal treatment*'.

[99]: Bjorge et al. (1985), 'Evaluation of Wolf Control to Reduce Cattle Predation in Alberta'

I will divide the comparison between France and North America in two steps: the effects at removal locations (*i.e.* the pasture or the wolf territory), and the effects on the area adjacent to these locations.

1. *The reduction at the removal locations*

Knowing the American context, I think the reduction of depredation at the site of culling application was almost inevitable given the high deployed removal intensity combined to the non-saturation of the wolf population. The large amount of time before the next depredation, from a median of 2 months to 2 years [96] after a successful intervention, reflects to me that the dynamic of replacement of wolves at a specific place is low.

Our results could show in three cases a brutal reduction of depredations at the site of application of culling: in the massifs of Cerces and Préalpes de Digne, and for simultaneous deaths of several wolves (mean of 2.2). The recurrence of attacks at Cerces and Préalpes de Digne was of ~ 55 days and ~ 40 days, respectively. This was not far from the findings of [96] for partial removals (mean of 2.2 too).

However, for most analysed contexts in our study, depredations were still observed, even when focusing only on the site of application. To me, this was due to the difference of wolf context between the two countries. In

the French Alpine Arc, we have seen wolf and pack density was high and the removal intensity was weak. Therefore, the risk for pack dissolution should be smaller. To be more specific, the low risk for pack dissolution depended on three parameters. First, **the risks to remove a breeder** under weak removal intensity should have been low. For example, there were 13 breeding females culled on 103 adult females from 2011 to 2020, regardless of culling type (unique, interacting etc...). With the increase in pack density in the Alps, the **pack size** was likely to increase too [31]; therefore, if a breeder was culled, this should have 1) minimised the risks for pack dissolution as large packs are less concerned by this process [174] and 2) increased the risks for multiple breeding in the same pack [156]. Moreover, even if pack dissolution occurred, the **saturation of the area** in wolves would accelerate the occupation of the territory by wolves from adjacent territories.

[31]: Mech et al. (2003), *Wolves: Behavior, Ecology, and Conservation*

[174]: Brainerd et al. (2008), 'The Effects of Breeder Loss on Wolves'

[156]: Ausband (2018), 'Multiple Breeding Individuals within Groups in a Social Carnivore'

I believe these three combined parameters made it more difficult for culling in France to be efficient in reducing depredations at the site of culling application compared to the USA. Thus, in the middle of the French Alpine Arc, it seems quite difficult to imagine that a pack removal would allow the absence of depredations for 2 years given the current wolf density and the population growth. Only in the zones outside of this region, culling events had led to full stops of depredations, because the culled wolves were living alone and were isolated from the rest of the population (*e.g.* the culled wolf in Costières de Nîmes, Gard, in 2019).

Other results: sex and deterrence

Contrary to [97], we did not find a difference of effects between females and males, maybe because we did not have enough variability to pool the culling events per sex and age class. We may have found a potential signal for deterrent effects, as the 6 missed shots of brigadiers on a group of wolves seemed to apparently reduce the depredations. This result was not found when the shot was missed for only one wolf in 13 cases. This maybe suggest that, if this missed wolf did not come back to pastures because of the shot, other wolves of its territory could still come because they did not live the deterrent effect of a missed shot. However, the too low number of operations involved do not allow us to confirm with confidence this result.

2. *The report or spread of risks on adjacent areas*

On the contrary, when considering the adjacent pastures, results suggested in some contexts reports or spreads of depredations[22]. This is consistent with findings from [52]. However, I found hard to explain the depredation reports or spreads by pack dissolution as they did, given what I think were minimised risks for this process in the French Alpine Arc. If this suspicion of report or spread was confirmed, I could see two ways to explain it, separately or combined.

First, the results I presented were corrected for pastoral use only. **Results were not corrected for the wolf life cycle dynamic**. Most culling events occurred during August–October. Food needs are increasing within a wolf territory from the birth of pups in spring to the autumnal dispersal. The increase in food needs, whether it is within the territory concerned by the culling events or in adjacent territories, could partly explain the spread or report of depredations. For example, if a culling event has no effect on the concerned territory, depredations would stay high or increase at the culling location, but also in adjacent packs due to their own food need increase. If a culling event has a reducing effect in the concerned territory (by killing wolves then reducing food needs and/or pup survival), then this would not prevent the adjacent packs to increase the depredations on their territories due to their own food need increase.

22: mostly around 5 km from culling events, but it could go up to 10 km. In comparison, a wolf territory radius was estimated at around 7–8 km in France in 2012 [115].

The second way to explain it would be that another process than pack dissolution was responsible for pack disruption. I especially think to multiple breeding. The saturation of the area in wolves, and the probable increase in wolf pack sizes, could quite match with an increase in natural multiple breeding events [155] [156]. It has been shown that the death

[155]: Ausband (2019), 'Pair Bonds, Reproductive Success, and Rise of Alternate Mating Strategies in a Social Carnivore'

of a breeder could lead to temporary multiple breeding [178]. Multiple breeding for example induced by culling would result in the upholding of the concerned territory, increasing the needs for this territory and therefore needs for dispersal too. Therefore, this could result in spreads of depredations. However, this does not remove the fact that legal culling of breeders was probably still weak considering the removal intensity in France. Nevertheless, I did not mention the possibility for illegal culling events. During August–October, legal culling events were frequent, but there were some reasons to think that poaching could be frequent too during this period (source: Coadapht). This could substantially increase the mortality of breeders, and therefore the increase of disruptions of packs and of multiple breeding, especially during this period (our results during July–August showed suspicion for depredation spread).

3.6 Conclusion

Chapter 3: Effects of culling on depredation

There is no binary answer to the question of the effects of culling on depredation in France. Applications and contexts of the analysed culling events were varied across space and time, whether these variations were linked to the environment, to pastoral practices or to the wolves. It is hopeless to seek an extraction of a general and unique tendency of the effect of culling of wolves on depredation for the French Alpine Arc, let alone at the global scale.

In response to these varied contexts, the effects of culling, according to their characteristics, varied. The majority of groups of culling events involved a reduction of depredations[23] or no change. Meanwhile, a minority of groups indicated an increase of depredations, especially according to the season of application. Spatial reports or spreads on adjacent pastures could be suspected for some groups of culling events too.

However, the profiles of the spatial and temporal distribution of depredations around culling events were never the same across groups. Each figure of result had to be thoroughly examined if it was of interest, and could not be summarised by a yes or a no. Nevertheless, knowing it could be long to go through all the figures one by one, I provided an attempt of synthesis of these results in a unique table, displayed in the general Discussion of the thesis, section *The kernel method* (Table 5.2). **I insist that this table is by no means a substitution to the kernel figures**.

Given my results and my interpretations, a comparison between this study and those focusing in North America is hardly relevant. I nonetheless provided in the discussion of this chapter, **clues to explain the differences between our situation and the situation in North America**. I notably highlighted some differences in the wolf population dynamics and environments between our study area and those in the USA, and how these differences could involve different biological processes, especially pack dissolution and multiple breeding.

23: More rigorously, it was the observed depredation intensities minus the depredation intensities expected by pastoral use.

Chapter Four

Hotspots of depredation 4

Preamble

The French authorities define each year hotspots as the municipality with a mean of at least 15 depredations over the last three years, and all the adjacent municipalities. Hotspots are called ***cercles 0*** (Figure 0.7). An administrative report [142] signalled in 2020, p.8: *'the conditions for the definition of* cercle 0 *are insufficiently narrow in time and space to faithfully reflect the reality of predation intensity (e.g. no reactivity to take into account the emerging phenomenons, grid too large that put aside small municipalities.)'*.

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4.1 Aim of the chapter

Understanding how depredations are structured in space and how this structure evolves through time is essential when managing depredations. Managers need to spot the areas where depredations are frequent, called *hotspots*, because the risk of conflicts is high in these areas [266, 267]. Identification of hotspots is required to plan the policy of the depredation management. Indeed, hotspot identification can be useful to plan the allocation of non-lethal subsidies, but also the authorisations for lethal removals. Finally, if some hotspots are persistent over time, managers can investigate the reasons of the persistence, support livestock owners in the implementation of non-lethal measures and prioritise the experimentation of new methods of protection, as it is planned in the current wolf management plan in France [77].

French authorities have so far focused on hotspots to manage the conflict by subsidising preventive measures in priority in hotspots, but also by recently conditioning the compensations to implementation of non-lethal measures for these hotspots (see section *Application of compensations in France* on 12). Definition of hotspots, as indicated in the preamble, is currently made according to the level and recurrence of depredation events at the municipality scale. The definition accounts neither for the surface of the municipality nor of the pastoral surfaces. Moreover, the definition does not account for the size of flocks or the time spent on pastures, both conditioning sheep risk exposure to depredation.

This chapter aimed at conducting spatial statistical analyses *1)* to investigate the temporal evolution of the summarised depredation spatial organisation (*i.e.* the mean distance over which depredations are aggregated) and *2)* to detect the annual hotspots of wolf predations on sheep at the pasture level. Both analyses focused on the French Alpine Arc from 1995 to 2018 and accounted for sheep risk exposure.

The goal of the first analysis was to understand if wolf territoriality could explain the depredation spatial pattern or not, and how this pattern changed in the course of wolf recolonisation. We also conducted this analysis in the Mercantour National Park only, where recolonisation in

[142]: Auvergne-Rhône-Alpes et al. (2020), *Rapport d'évaluation de l'arrêté Ministériel Expérimental Du 26 Juillet 2019 Portant Expérimentation de Diverses Dispositions En Matière de Dérogation Aux Interdictions de Destruction Pouvant Être Accordées Par Les Préfets de Département Concernant Le Loup (Canis Lupus)*

[266]: Abade et al. (2014), 'Assessing the Relative Importance of Landscape and Husbandry Factors in Determining Large Carnivore Depredation Risk in Tanzania's Ruaha Landscape'

[267]: Miller (2015), 'Mapping Attack Hotspots to Mitigate Human–Carnivore Conflict'

[77]: MTES et al. (2018), *Plan National d'Actions 2018-2023 sur le loup et les activités d'élevage*

France by wolves started in the 1990s, in order to explore the spatial pattern at a local scale.

The second analysis is directly directed towards a proposition of improvement in the method of hotspot identification in France. Moreover, the goal was also to complete the first analysis by observing the number, the variations in size and the locations of these hotspots in the French Alpine Arc.

The study of this chapter is currently under review in *Biological Conservation*:

> Oksana Grente, Thibault Saubusse, Olivier Gimenez, Eric Marboutin and Christophe Duchamp (2021). Wolf depredation hotspots in France: Clustering analyses adjusting for livestock availability. *EcoEvoRxiv*. DOI:10.32942/osf.io/n8rzg.

In comparison to the preprint in EcoEvoRxiv, I added some figures and green boxes of synthesis in this chapter.

To sum up

The main aim of this chapter was twofold. First, the goal was to understand how depredations of wolves were distributed throughout space: Were they aggregated? If yes over which distance? Were they always aggregated at the same place? Did this spatial pattern change through wolf's recolonisation of the French Alpine Arc? Second, the study should be seen as a proposition of a management tool or a decision help that is more adapted to detect hotspots, mainly because the analysis is conducted at a small scale in space and time, and above all because the analysis adjusted for sheep risk exposure.

4.2 Literature review

To understand the spatial and temporal patterns of depredation, two complementary approaches can be applied, namely the spatial correlation analysis and risk modelling. The spatial correlation analysis quantifies the level of clustering or regularity (*i.e.* repulsion) of a depredation pattern [257, 268] and enables the identification of hotspots or coldspots where events are unusually aggregating or scarce, respectively. Risk modelling aims at estimating the spatial risk of depredation, by quantifying the relationship between ecological or non-ecological features and depredation numbers or occurrences [267].

The spatial correlation analysis is often presented as a preliminary step to risk modelling and as of limited interest if applied alone [268] [269]. This may explain why risk modelling is more popular (*e.g.* [55, 270, 271]) than spatial correlation analyses in the scientific literature. However, risk models only reflect the depredation-factor relationships at a given point in time and space. These relationships may evolve because predator-prey systems are dynamic and carnivores can adapt their predation behaviour according to environmental or livestock management changes [267]. This is especially true for (re)colonising large carnivore populations of plastic species such as the grey wolf (*Canis lupus*) which can embrace a large

[257]: Baddeley et al. (2015), *Spatial Point Patterns: Methodology and Applications with R*

[268]: Hoffmann et al. (2019), 'Spatial Pattern Analysis Reveals Randomness Among Carnivore Depredation of Livestock'

[269]: Gastineau et al. (2019), 'Spatiotemporal Depredation Hotspots of Brown Bears, Ursus Arctos, on Livestock in the Pyrenees, France'

[55]: Bradley et al. (2005), 'Assessing Factors Related to Wolf Depredation of Cattle in Fenced Pastures in Montana and Idaho'

[270]: Fowler et al. (2019), 'Non-Linear Relationships between Human Activities and Wolf-Livestock Depredations'

[271]: Balbuena-Serrano et al. (2021), 'Hotspots of Livestock Depredation by Pumas and Jaguars in Brazil: A Biome-Scale Analysis'

range of habitats [31, 272]. Risk models developed for this species were either restricted to a unique region and type of habitat (*e.g.* [273]) or showed a low predictive power when applied to habitats that differ from those originally used in the analysis [236]. Therefore, the outcomes of risk models are hardly transposable to other areas or on long-term periods, which makes their adoption by managers difficult [267]. In contrast, information about current or past hotspot locations provided by spatial correlation analyses can directly help managers when allocating conservation resources such as subsidies of preventive measures or when investigating the causes of depredation *in situ*. Prioritising conservation efforts on depredation hotspots is indeed recommended as recurrences of high levels of attacks in the same areas are likely to trigger negative attitudes [274].

[31]: Mech et al. (2003), *Wolves: Behavior, Ecology, and Conservation*

[272]: Llaneza et al. (2012), 'Insights into Wolf Presence in Human-Dominated Landscapes: The Relative Role of Food Availability, Humans and Landscape Attributes'

[273]: Clark et al. (2020), 'Predicting Spatial Risk of Wolf-Cattle Encounters and Depredation'

[236]: Hanley et al. (2018), 'Forecasting Cattle Depredation Risk by Recolonizing Gray Wolves'

[274]: Stahl et al. (2001), 'Predation on Livestock by an Expanding Reintroduced Lynx Population'

So far, several analyses of spatial correlation have been developed to identify depredation hotspots. The simplest one consists in defining an arbitrary threshold for a selected indicator like the number of depredations which, if reached, turns the spatial unit into a hotspot. Units can be administrative areas (*e.g.* [275]) or simple shapes like circles [274]. To avoid arbitrary thresholds, some studies have applied spatial statistical analyses (*e.g.* [268, 269] [276]) where depredation events were considered as a spatial point pattern, *i.e.* a dataset of observed spatial locations of a biological process [257]. The areas exhibiting significantly more depredation events than expected under Complete Spatial Randomness (CSR) were statistically identified as hotspots. To gain understanding of the biological process, the spatial statistical analyses can also be conducted to determine the summarised spatial structure of the pattern, *i.e.* the range of distances over which the pattern generally exhibits clustering, randomness or regularity [257] (*e.g.* [277]).

[275]: Dhungana et al. (2019), 'Livestock Depredation by Leopards around Chitwan National Park, Nepal'

[276]: Packer et al. (2019), 'Species-specific Spatiotemporal Patterns of Leopard, Lion and Tiger Attacks on Humans'

[277]: Kushnir et al. (2014), 'Using Landscape Characteristics to Predict Risk of Lion Attacks on Humans in South-Eastern Tanzania'

However, these quantitative studies did not control for spatio-temporal livestock availability because the statistical method they used did not allow it or because the relevant data were not available. Yet the spatial pattern of depredation is inherent to livestock risk exposure. Not only are conflicts exclusive to areas where carnivore and livestock distributions overlap, but they are also dependent on livestock availability, which is itself a by-product of livestock counts and time spent in a specific area. If livestock availability is ignored, it is difficult to disentangle the hotspots based on high levels of livestock availability from the hotspots where sheep exposures are low but depredation rates disproportionally high. In the latter cases, conflicts may be favoured by factors linked to, *e.g.*, the environment, the predator or the husbandry practices which can be identified and managed to some extent.

Discrepancy between research and management

Models predicting the depredation hotspots according to environmental or pastoral factors are commonly found in the scientific literature. We believe the correct identification of current hotspots is more useful for managers. To date, no study on depredation hotspot identification has used or demonstrated the need to correct for livestock risk exposure to provide useful results for management.

4.3 Databases

Study area and study period

The study area covered the two south-east regions of France, Auvergne-Rhône-Alpes and Provence-Alpes-Côte-d'Azur (hereafter AURA-PACA), and included all the French Alps and the east part of Massif Central mountains (102 483 km^2, Figure 4.1). Apart from the highest altitudes which are without forests, habitats range from bush to coniferous forest under Mediterranean climate in the south, to mixed forest in the north and the east.

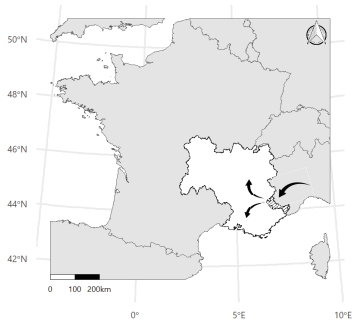


Figure 4.1: Location of the study area (white) within France, and of the MNP (hatched) within the study area, from which wolves from Italy recolonised France (black arrows). Credits: O. Grente

We analysed the summarised spatial structure of the depredation pattern at two scales of the study area. First, the analyses were applied over the whole study area, *i.e.* the regional scale. Second, the analyses were applied over a sub-area of the study area, located in the very south-east of the study area (2 146 km^2, Figure 4.1), *i.e.* the local scale. The local scale overlapped the Mercantour National Park and its surroundings (hereafter MNP), which is a mountainous area characterised by a succession of alpine vegetation levels along a wide altitudinal range, from 600 to 3 200 m, and by an important pastoral activity for meat production. The MNP is the oldest place where wolves and pastoralism are co-occurring in the country since wolf recolonisation in the 1990's from Italy.

In accordance with wolf biology, we defined the annual periods over which the analyses were applied as biological years y, starting from the 1st of April of year $y-1$ (*i.e.* wolf pup birth) to the 31st March of year y. The whole study period covered biological years (hereafter, 'years') from 1995 to 2018.

The study...

- encompassed the two administrative regions Provence-Alpes-Côtes-d'Azur and Auvergne-Rhône-Alpes in south-east France,
- analysed independently each year y from 1995 to 2018, each year beginning in April of year $y-1$ to March of year y.

Depredation records

Approximately three quarters of the depredations occurred between June and October, when most of sheep flocks were grazing in pastures. Up to 2019, the French Ministry of Ecology compensated for any killed farmed animal for which wolf responsibility could not be discarded, regardless of protective measures. Each claim was controlled and checked in the field by an accredited governmental agent who used a standardized protocol [115]. Therefore, most if not all depredations were reported if noticed, and the risk of false claims was low. We restricted the clustering analyses to depredations on sheep only as they constituted 90% of depredations on livestock. An event of depredation corresponded to at least one killed or wounded sheep by wolves. Because grazing activity may extend outside the official pastoral limits, or because of geolocation approximations, some depredation events were not located inside the geolocated pastoral surfaces (22% of the annual dataset on average).

[115]: Duchamp et al. (2012), 'A Dual Frame Survey to Assess Time– and Space–Related Changes of the Colonizing Wolf Population in France'

We excluded the depredations farther away from 500 meters of any pastoral surface (10% of the annual dataset on average) and assigned the remainder to the nearest pastoral surface.

We analysed only depredations...

- on sheep, regardless of the number of killed sheep,
- and located less than 500 meters from a pasture.

Wolf distribution

The *Réseau Loup-Lynx* managed by Office Français de la Biodiversité is in charge of the national wolf monitoring in France. Its field experts are trained to opportunistically collect presence signs all year along, such as biological samples (mainly faeces, combined with genetic analysis), tracks or direct observations, which are geolocated and validated according to a standardized protocol [115, 278]. The annual wolf distribution was determined by combining the annual presence signs and all wolf depredations (*i.e.* on any type of livestock, including all those located outside the pastures) within the study area. Wolf presence during year y was reported on a 10×10 km cell grid, and defined as the collection of at least one presence sign or one depredation in the cell from $y-1$ to $y-3$ and from $y-2$ to y (see [279]).

[279]: Marboutin et al. (2011), 'On the Effects of Grid Size and Shape When Mapping the Distribution Range of a Recolonising Wolf (Canis Lupus) Population'

The annual wolf distribution was based on...

- the wolf presence signs collected by *Réseau Loup-Lynx*
- and verified depredations.

Spatio-temporal sheep availability

Around 1 500 000 sheep are bred for meat or milk production each year in the study area [280]. During the summer period, a large part of these flocks becomes transhumant and moves to high-altitude pastures in the Alps. Otherwise, sheep are grazing in low- or mid-altitude pastures around farms. Sheep are in sheds during the whole winter except in the south where climate is mild [281].

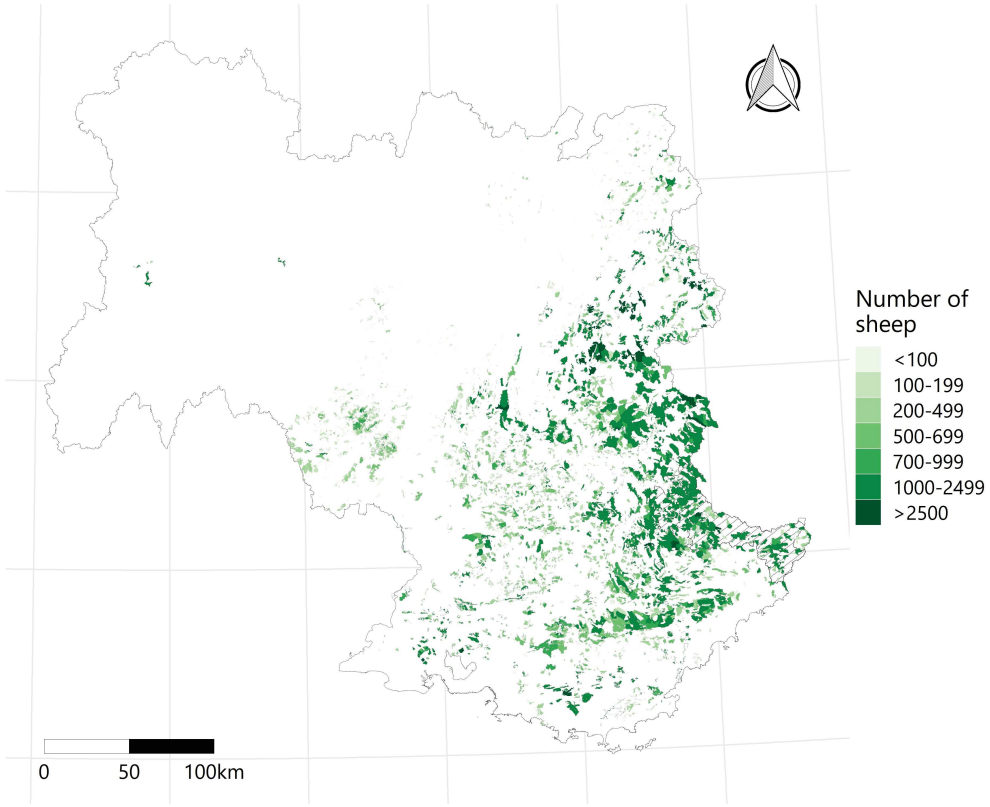
[280]: IDELE (2018), *Ovins 2017 Productions lait et viande*

[281]: Gervasi et al. (2021), 'Ecological Correlates of Large Carnivore Depredation on Sheep in Europe'

Two georeferenced censuses of the pastoral surfaces in the study area were carried out in 1996–1997 and in 2012–2014 by IRSTEA[1]. For each pastoral surface, information about the grazing livestock count per species and the annual number of grazing days was included. One or several herds, of one or multiple livestock species, could feed on a pastoral surface. We restricted the dataset to pastoral surfaces with grazing sheep, regardless of whether other species of livestock were present. For both censuses, the spatio-temporal sheep availability was inhomogeneous across the study area (Figure 4.2), particularly for grazing time between the north and the south of the regional scale due to climate differences and resulting grass phenology. The pastoral surfaces of the first census and of the second census were respectively 2.7 km^2 and 1.9 km^2 on average, and they hosted 606 sheep ($sd = 649$) and 516 sheep ($sd = 547$), during 146 days ($sd = 96$) and 202 days ($sd = 96$) per year on average.

1: National Research Institute of Science and Technology for the Environment and Agriculture

(a) Annual grazing sheep count



(b) Annual number of grazing days

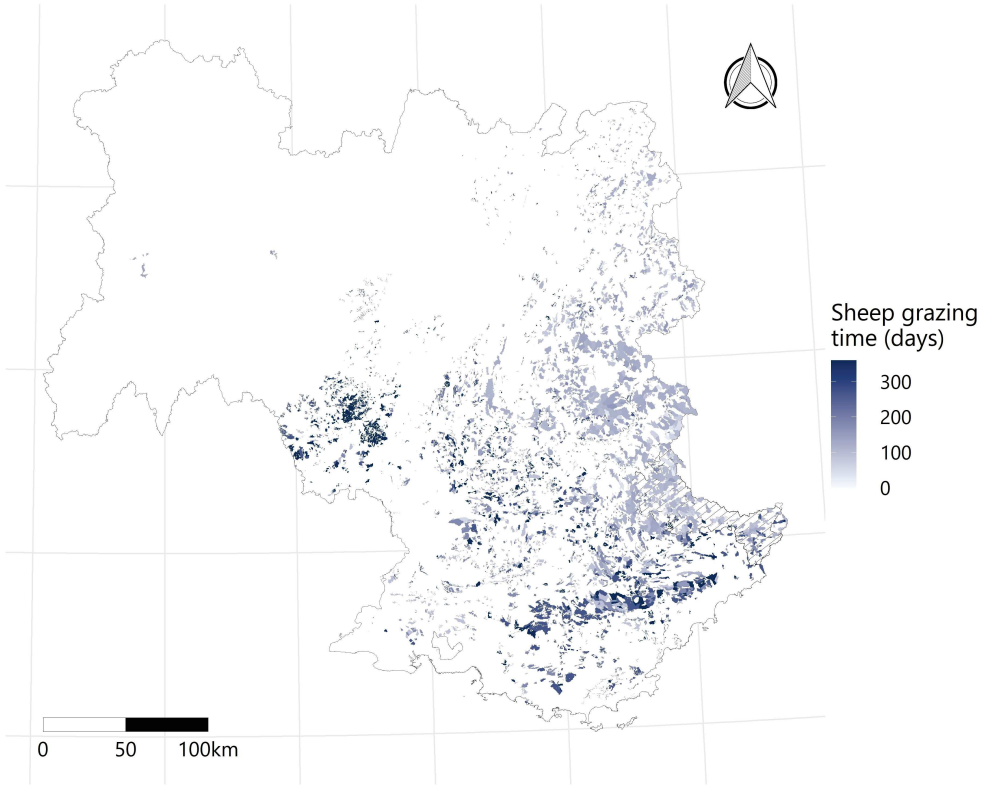


Figure 4.2: Characteristics of the pastoral surfaces according to the 2012-2014 census of the study area, including the MNP (hatched). Visualisation of the information for 1996-1997 census in Figure D.1 or at or at https://oksanagrente.shinyapps.io/Hotspots-SuppFig1/. Credits: O. Grente

For each year y, we identified the set of pastoral surfaces at depredation risk for both scales by selecting the pastoral surfaces which overlapped, even partially, with the wolf distribution. For years between 1995 to 2005, we used the 6 488 pastoral surfaces with sheep from the oldest census, and for years between 2006 to 2018, we used the 12 438 pastoral surfaces with sheep from the latest census. The oldest census did not include pastures in the west of the study area (*i.e.* outside the Alpine area), which explains the lower number of pastures compared to the latest census. However, the wolf distribution from 1995 to 2005 was mainly restricted to the east of the study area, within the Alpine area (Figure 4.3), where pastoral information in the oldest census was available. For example, using the latest census instead of the oldest census only provided a difference of 6.7% on average in the numbers of pastoral surfaces at depredation risk at the regional scale from 1995 to 2005. Thus, we considered this gap was of little impact.



You can access an online version of Figure 4.2 in Figure D.1 or at https://oksanagrente.shinyapps.io/Hotspots-SuppFig1/. Figures for the 1996-1997 census are also available.

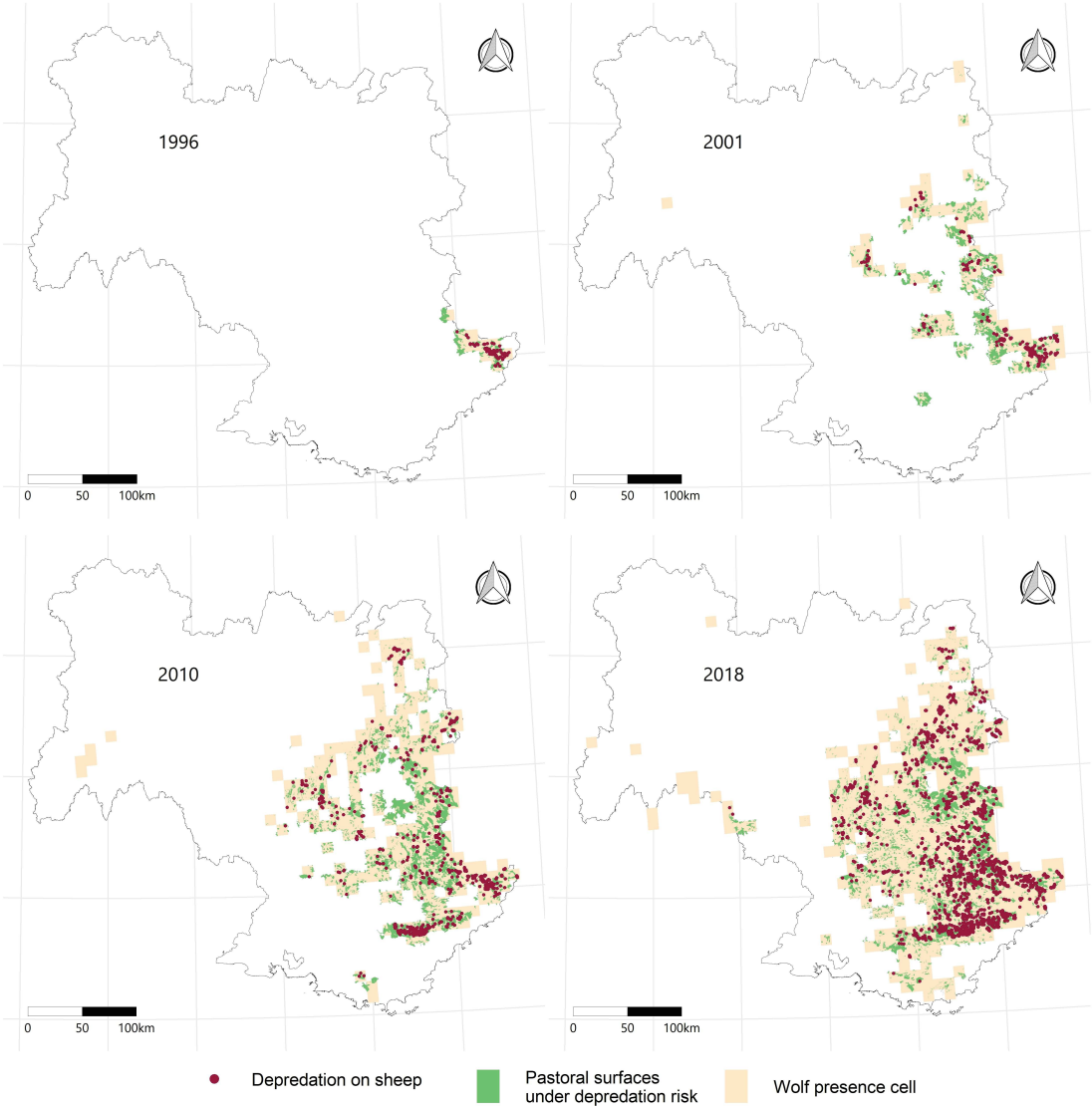


Figure 4.3: Annual distributions of wolf presence, pastoral surfaces at depredation risk and verified wolf depredations on sheep in the study area for biological years 1996, 2001, 2010 and 2018. All years are available in the interactive version at https://oksanagrente.shinyapps.io/Hotspots-SuppFig2/ (Figure D.2). Credits: O. Grente

IRSTEA did not carry out the census process every year for two reasons. First, the census process was the result of a long period of work, exceeding a year of work. The field work, which consisted in meetings with local contact persons, corresponded to 750 full working days on its own for the second census (F. Bray, *pers. com.*). Second, the use of pastoral surfaces by farmers was relatively stable over time, because the environmental characteristics (area, topography, type of vegetation, weather...) of a pasture restricted the herd size the pasture could host and the time of grazing. Moreover, the large but limited number of pastures caused hard competition between livestock owners for access to pastoral resources. Livestock owners tended to secure their access by renting or buying these surfaces for a long period of time (C. Duchamp, *pers. com.*). For all these reasons, we assumed the information on sheep availability of a census was valid for several years before and after the census.

We used pastoral information...

- about the counts of grazing sheep,
- and the number of grazed days for each pastoral surface,
- from the first IRSTEA census of 1996–1997 for the analysed years from 1995 to 2005,
- and from the second IRSTEA census of 2012–2014 for the analysed years from 2006 to 2018.

4.4 Analysis

Analysis 1: Summarised spatial structure of wolf depredations

For each year y, we analysed at the regional and local scales the summarised spatial structure of the wolf depredation pattern considering sheep availability by using K_{inhom} [257]. We used the package *spatstat* [261] in R 4.0.2 [193] to perform the analysis.

[261]: Baddeley et al. (2005), 'Spatstat: An R Package for Analyzing Spatial Point Patterns'
[193]: R Core Team (2020), *R: A Language and Environment for Statistical Computing*

First, we simulated the expected depredation pattern under CSR[2] considering sheep availability. The simulated pattern was composed of n points called '*controls*', in opposition to the n annual observed depredations called '*cases*'. The distribution of controls was simulated on a grid of 200×200 m cells over the pastoral surfaces at depredation risk, according to an inhomogeneous Poisson Point Process (PPP). In this model, the number of controls falling into a cell g was expected to be equal to the intensity $\lambda(g)$ defined as:

2: Complete Spatial Randomness

$$\lambda(g) = exp(a + b \times log(pop_u) + c \times log(time_u)) \tag{4.1}$$

where pop_u and $time_u$ were the numbers of sheep and of grazing days of the pastoral surface u covered by cell, g and a, b and c were parameters to be estimated. Covariates were log-transformed because of their skewed distributions. Thus, the controls were more likely to fall into the cells covering pastoral surfaces with high numbers of pop_u and $time_u$. For each year, we simulated 499 control patterns through this model.

Second, we computed K_{inhom} for the pattern of n cases. This function drew a circle of radius r around each depredation i covering more or less neighbouring depredations $\{j\}$. Then, the function summed the values $1/(\lambda(g_i)\lambda(g_j))$ for all pairs of depredations $i - j$ within this circle, $\lambda(g_i)$ and $\lambda(g_j)$ being the intensity values of the cell(s) containing i and j respectively. Because the unit of measurement of λ was in ind/cell (*i.e.* ind/0.04km^2), K_{inhom} returned a surface for each tested r. If the pattern was randomly distributed considering sheep availability, the surface should equal the surface of the circle, πr^2. Consequently, at a specific r, if the K_{inhom} value of the observed depredation pattern was higher or lower than πr^2, we could conclude that the depredations were respectively forming hotspots or coldspots of radius r. A large set of continuous radiuses r was tested.

However, the smaller the dataset, the larger the likelihood of differences from the expected number of points within a circle, even if the dataset has a random pattern. Therefore, a K_{inhom} value which differed from πr^2 was not necessarily the result of a non-randomly point pattern, but could be due to stochastic effects. To take this into account, we also computed K_{inhom} for the 499 control patterns and selected the 50th-lowest and 50th-highest values to build a control envelope. For a specific r, if the observed K_{inhom} was higher (or lower) than the upper (or lower) envelope limit, the depredations were significantly clustered (or regular, *i.e.* tended to avoid each other) at this distance considering sheep availability. The larger the differences with the envelope, the more aggregated or regular the pattern.

We also annually applied the K-function at the regional scale. The PPP of the K-function was homogeneous. Hence, the number of controls falling into the cells was expected to be equal over the whole analysis area [257]. We tested two possibilities to define the grid of 200 × 200 m cells. First, we simulated the same grid over the pastoral surfaces at depredation risk as in the K_{inhom} analysis, in order to simulate a situation for which sheep distribution was known, but sheep availability was not. Second, we simulated the grid over the wolf distribution, to simulate a situation for which the pastoral data were totally unavailable.

The K_{inhom} function...

- was computed for each year y, only with pastoral surfaces within the wolf distribution,
- simulated random depredations whose distribution was depending only on the flock size and the grazing time of pastoral surfaces,
- compared the differences of distribution between the observed depredations and the simulated ones,
- to know if the observed depredations are aggregated (or the opposite) and over which distances.
- and did not produce a map, only a summary of the depredation spatial pattern.

Analysis 2: Wolf depredation hotspot location

For each year y, we located at the regional scale the significant wolf depredation hotspots by applying the first version of the *Kulldorff* statistic [282] which adjusts for spatially inhomogeneous population at risk. We used the package *SpatialEpi* [283] in R 4.0.2 [193] to perform the analysis.

[282]: Kulldorff (1997), 'A Spatial Scan Statistic'
[283]: Kim et al. (2018), *SpatialEpi: Methods and Data for Spatial Epidemiology*

First, we defined all the possible zones Z which could be later identified as hotspot by the *Kulldorff* statistic. We defined the pastoral surface as the smallest possible zone Z. Then, a circle was put on the centroid of each pastoral surface, with a progressively increasing radius. Each time the growing circle encompassed the centroid of an adjacent pastoral surface, a new zone Z was defined. The sheep availability of a zone Z was calculated as the sum of the sheep availability $\omega(u)$ of all the pastoral surfaces u whose centroids were in Z. We determined the limit size of a zone Z as following: a zone Z could not include more than 5% of the sum of $\omega(u)$ of all pastoral surfaces. Otherwise, the hotspots were too vast to be informative [282]. Because information on the pastoral area was omitted in this analysis, we included this information in the definition of the sheep availability of a pastoral surface $\omega(u)$, as $\omega(u) = pop_u \times time_u \times area_u$, where $area_u$ was the surface u in km^2. Therefore, the larger a pastoral surface, the larger its risk of depredation. We indeed considered that two flocks of the same size and grazing time should have a different depredation risk depending on the size of their pastures. Farmers generally used the entire pasture for their flock, either by dividing the flock into smaller flocks or by moving the flock within the pasture. Increasing the pasturing area should make the flock more exposed to depredation by increasing the risk of encounters with wolves. In addition, we restricted the analysis to the depredated pastoral surfaces. The inclusion of pastoral surfaces without depredation into the analysis indeed increased sheep availabilities of certain zones, especially zones where depredated pastoral surfaces were surrounded by pastoral surfaces without depredation. This reduced the capacity of the analysis to identify such zones as hotspots.

Second, the *Kulldorff* statistic modelled the total number of observed depredations n as:

$$n \sim Poisson(p_z \times \omega(u \in Z) + q_z \times \omega(u \notin Z)) \tag{4.2}$$

with the probabilities p_Z and q_Z that a depredation event occurred within or outside Z, respectively, and $\omega(u \in Z)$ and $\omega(u \notin Z)$ the sum of $\omega(u)$ inside and outside Z, respectively. For each Z, the *Kulldorff* statistic tested the null hypothesis $p_Z = q_Z$ (M_0) and the alternative hypothesis $p_Z > q_Z$ (M_A). It calculated the likelihood ratio $LR(Z)$ as $\frac{L(Z)}{L_0}$. $L(Z)$ corresponded to the result of the likelihood function L of the model under M_A for the zone Z. L_0 corresponded to the result of the likelihood function L of the model under M_0, which was the same for all zones because under M_0 the model can be reduced to $n \sim Poisson(p \times \sum(\omega(u))$. The zones Z for which M_A was the most likely had the highest $LR(Z)$.

Third, we simulated 499 sets of randomly distributed n controls over the depredated pastoral surfaces, proportionally to their sheep availability.

The second step was repeated for each control set, to eventually compute the control distribution of the highest likelihood ratio $LR(Z)$. If the observed highest $LR(Z)$ were among the top 5% of this control distribution, then these zones were significant hotspots.

We repeated this analysis with a simulated homogeneous sheep availability to show the discrepancies when ignoring prey availability: each depredated pastoral surface had then a sheep availability equal to the mean observed sheep availability of the depredated pastoral surfaces.

The *Kulldorff* statistic...

- was computed for each year y, only with pastoral surfaces with depredations,
- was a statistical test which grouped adjacent pastoral surfaces together, testing different sizes of gathering,
- and compared the likelihood that a depredation occurred within each group rather than outside,
- to identify the hotspots amongst these groups.

4.5 Results

Trends in depredation risk and observed depredations

We collected 25 220 wolf presence signs and 18 764 verified depredations on any type of livestock, reported from 1995 to 2018 in the study area. The resulting estimated annual wolf distribution expanded along the years, and reached 40% of the study area in 2018 (Figure 4.4.A). The annual proportion of pastoral surfaces at depredation risk within the total set of pastoral surfaces increased at the regional scale, reaching 70% in 2018. This overlap generated more and more depredations on sheep per year, starting from 49 depredation events in 1995 to 2 289 in 2018. However, the annual proportion of depredated pastoral surfaces among all surfaces at risk remained quite stable over time at the regional scale, with a mean of 18%. Most of these pastoral surfaces experienced one or two depredations per year (Figure D.3). One depredation event corresponded on average to 3.8 wounded or killed sheep ($sd = 0.3$) when removing indirect mortalities.

The situation at the local scale differed (Figure 4.4.B). The majority of the local scale was recolonised by wolves from 2003. Most depredated pastoral surfaces also experienced one or two depredations per year (Figure D.3). Because the number of pastoral surfaces at depredation risk quickly stabilised, the trend of the depredation numbers followed the trend of the proportion of depredated pastoral surfaces.

Different trends according scales

- Recolonisation by wolves was complete in the MNP since 2003, but not in AURA-PACA.
- Depredations stabilised in the MNP since 2013, but were still increasing in AURA-PACA.

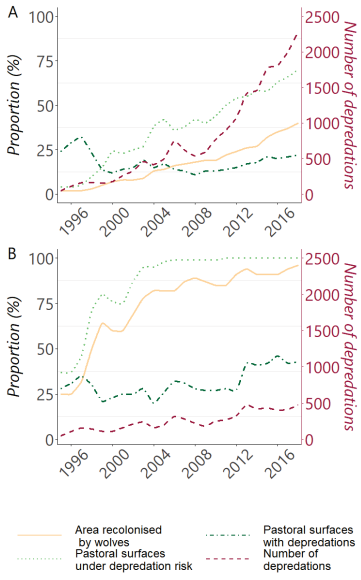


Figure 4.4: Proportion of 10x10km cells of the study area within wolf distribution (solid yellow), proportion of pastoral surfaces within wolf distribution in the whole set of pastoral surfaces (dotted light green), proportion of pastoral surfaces with at least one reported wolf depredation on sheep in the set of pastoral surfaces within wolf distribution (dot-dashed dark green), and number of wolf depredations on sheep (dashed red) per year in the area. At the A) regional scale, B) local scale. Credits: O. Grente

Analysis 1: Summarised spatial structure of wolf depredations

At the regional scale, the K_{inhom} function identified significant aggregation of the depredations for all years, with some K_{inhom} values higher than the control envelope (Figure 4.5, Figure D.4). The control envelope was thinner with time as the depredation pattern included more and more events. However, depending on years, the range of radiuses r for which aggregation was significant varied, as well as the aggregation intensity (*i.e.* difference between the observed and control envelope values at the same r). We identified four time periods.

The first period ranged from 1995 to 1999. In 1995, aggregation was significant up to 20 km. The depredation pattern exhibited randomness beyond. From 1996, aggregation was significant for the whole range of computed radiuses r, up to 15-30 km around depredations. Aggregation tended to intensify with r, especially in 1996 and 1998. This suggested that the depredation pattern showed no particular spatial structure, except in 1995. **During the second period from 2000 to 2003**, aggregation intensity decreased at the largest computed r values. From 2001, the K_{inhom} values merged with the control envelope between 40 and 50 km, suggesting a locally emerging clustered pattern. **During the third period from 2004 to 2012**, a weak significant aggregation was only observed

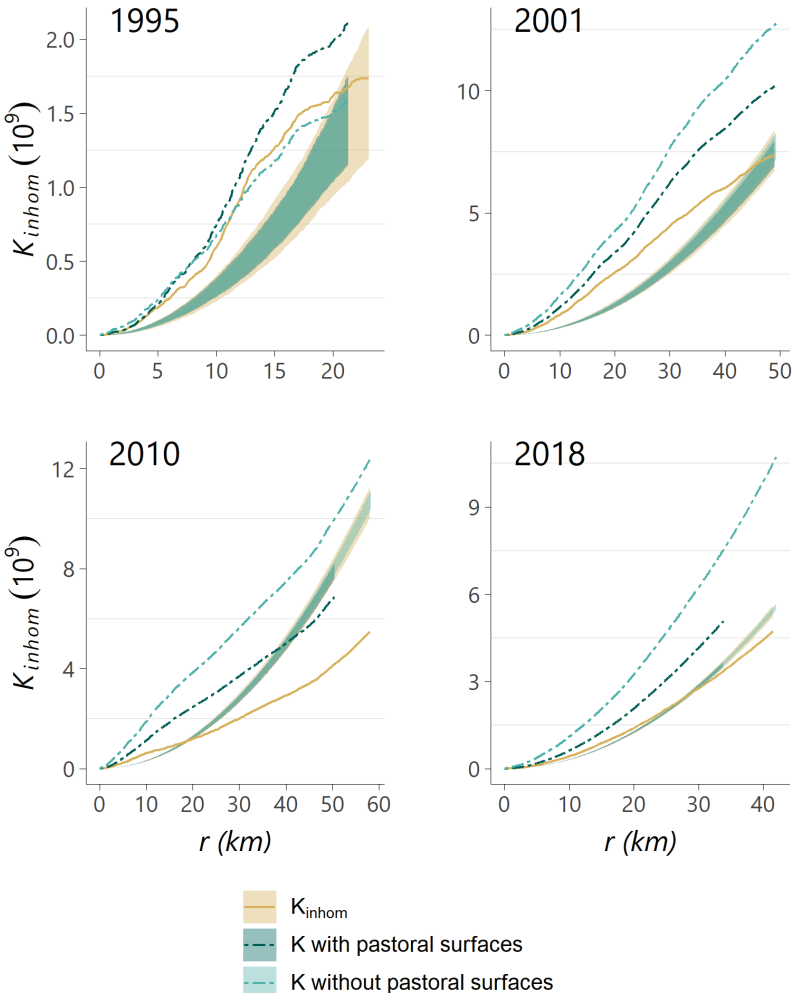


Figure 4.5: Results at the regional scale of the K_{inhom} function (solid yellow line) and of the K-function where the analysis grid was simulated over the pastoral surfaces at depredation risk (dotted dark blue line) or over the wolf distribution (dotted light blue line), against their corresponding control envelopes, for years y 1995, 2001, 2010 and 2018. The r distances were limited in the figure to those computed by the K_{inhom} function. Results for all years y and for all computed r are available in the interactive version (Figure D.4). Credits: O. Grente

over the lowest r values, and turned into significant repulsion between 15 and 35 km. This was typical of a clustered pattern, with hotspots producing coldspot interzones [268]. Finally, **the last period from 2013 to 2018** showed significant aggregation over 25 to 40 km followed by randomness (except 2014 with continuous aggregation). In certain years, a weak repulsion was observed at the largest r values. Aggregation intensity was greater in 2013 compared to 2012, but it tended to decrease the following years, which brought the depredation pattern closer to randomness with time.

Using K_{inhom} or K provided comparable results only during the first period. But, from 1999-2000, the differences between the analysis of K_{inhom} and the two analyses of K increased (Figure 4.5, Figure D.4). The first analysis with K-function which considered sheep availability as homogeneous across pastoral surfaces identified the typical hotspot structure (*i.e.* aggregation followed by repulsion) only in 2009 and 2010 with a radius of 30 and 40 km respectively. The other years, aggregation was significant for all values of r and always more intense than the one obtained through K_{inhom}. When the analysis grid was only based on the wolf distribution, the K-function analysed the pattern over larger values of r than the previous analyses because isolated distribution cells in the west of the study area could sporadically appear without overlapping with pastoral surfaces. This analysis only identified significant aggregation which, in most years, intensified with r.

At the local scale, the K_{inhom} function provided two main findings. First, from 1995 to 2011, the analysis identified significant aggregation over 12 to 17 km, occasionally followed by randomness at large radiuses (Figure 4.6a,

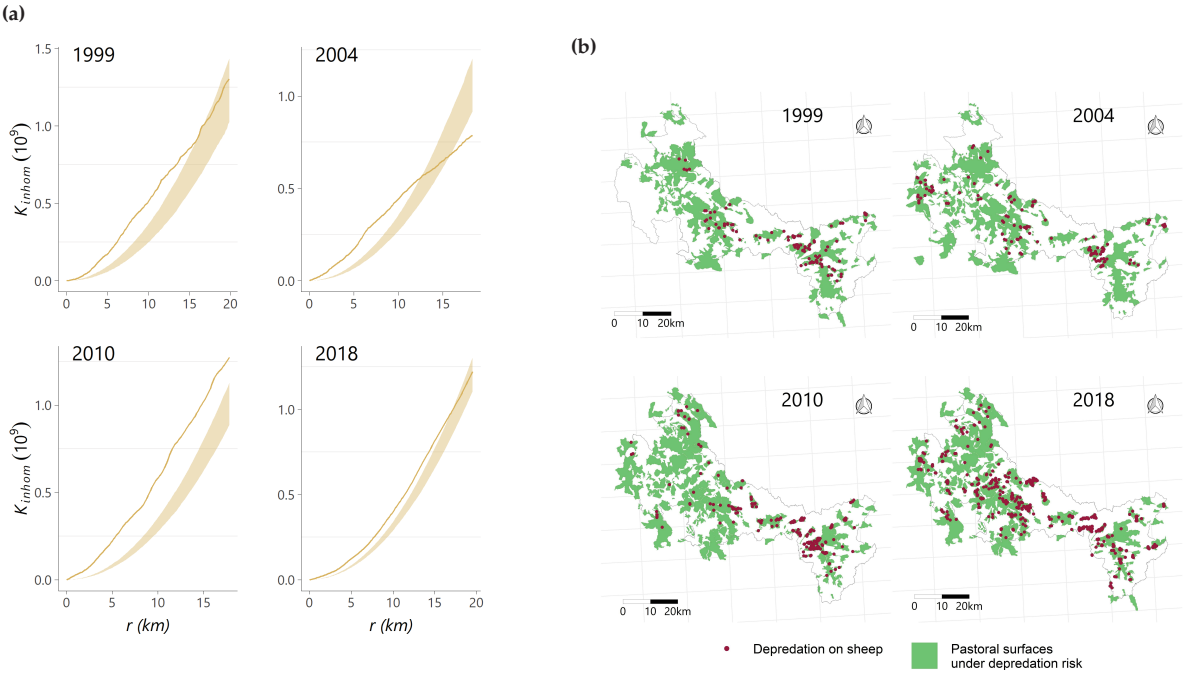


Figure 4.6: (a) Results at the local scale of the K_{inhom} function, against its corresponding control envelope, for years 1999, 2004, 2010 and 2018. Results for all years are available in the interactive version at https://oksanagrente.shinyapps.io/Hotspots-SuppFig4/ (Figure D.4). (b) Annual distributions of pastoral surfaces at depredation risk and of verified wolf depredations on sheep at the local scale for the years 1999, 2004, 2010 and 2018. Results for all years are available in the interactive version at https://oksanagrente.shinyapps.io/Hotspots-SuppFig2/ (Figure D.2). Credits: O. Grente

Figure D.4). Repulsion was never observed, except in 2004 (Figure 4.6a) where depredations seemed clustered into three single zones (Figure 4.6b). Second, the aggregation intensity was generally decreasing with time from 2013, even though the control envelopes were of equivalent thickness. The pattern tended to randomness for all values of r from 2015, with almost complete randomness observed in 2016. Therefore, the depredations were increasingly widespread at the local scale and were no longer significantly clustering in the last years of the study period, long after the full recolonisation of the MNP by wolves.

The K_{inhom} function...

- showed for AURA-PACA a progressive clustered pattern up to 2012, and a homogenisation of depredations since 2013,
- showed for MNP aggregated depredations up to 2015, then homogenisation,
- provided different results when the sheep risk exposure was not taken into account.

Analysis 2: Wolf depredation hotspot location

The number of hotspots identified by the *Kulldorff* statistic adjusting for sheep availability tended to increase over time in the study area, from 2 hotspots in 1995 to 32 in 2018 (Figure 4.7.A). The annual proportion of depredated pastoral surfaces into hotspots was higher for the period 2012–2018 ($mean$ = 29.2%, sd = 3.8%) than for the period 1995–2011 ($mean$ = 23.5%, sd = 5.9%) (Figure 4.7.B). Hotspots were of various sizes but generally did not exceed 50 km^2 of pastoral area (Figure 4.7.C). The average number of pastoral surfaces within hotspots tended to increase with time, from 3.0 in 1995 (sd = 0) to 7.8 in 2018 (sd = 11.5). Hotspots could be located at different places within the study area (Figure 4.8.A; Figure D.5). They could be sporadic, appearing for one year. But others could persist over time, such as in the MNP where hotspots were present during the whole study period, and in the south for the period 2013-2018.

In contrast to the analysis adjusting for sheep availability (hereafter 'first *Kulldorff* analysis'), the results of hotspot identification changed in the analysis with simulated homogeneous sheep availability (hereafter 'second *Kulldorff* analysis'). For almost all years, the numbers of hotspots were lower in the second *Kulldorff* analysis than in the first one (Figure 4.7.A). The annual proportion of depredated pastoral surfaces into hotspots was always lower in the second *Kulldorff* analysis and exceeded 20% only in 2014 and 2017 (Figure 4.7.B). The pastoral surfaces identified as hotspots in the second *Kulldorff* analysis were generally identified as hotspots in the first *Kulldorff* analysis (*e.g.* Figure 4.8.B; Figure D.5). The unidentified hotspots in the second *Kulldorff* analysis generally encompassed small pastoral surfaces where sheep availability was low as well as the number of depredations. Thus, annual means of sheep counts, of grazing time and of depredations of the pastoral surfaces within hotspots were significantly larger in the second *Kulldorff* analysis than in the first one (Wilcoxon tests: $P < 0.001$, $\alpha = 0.05$).

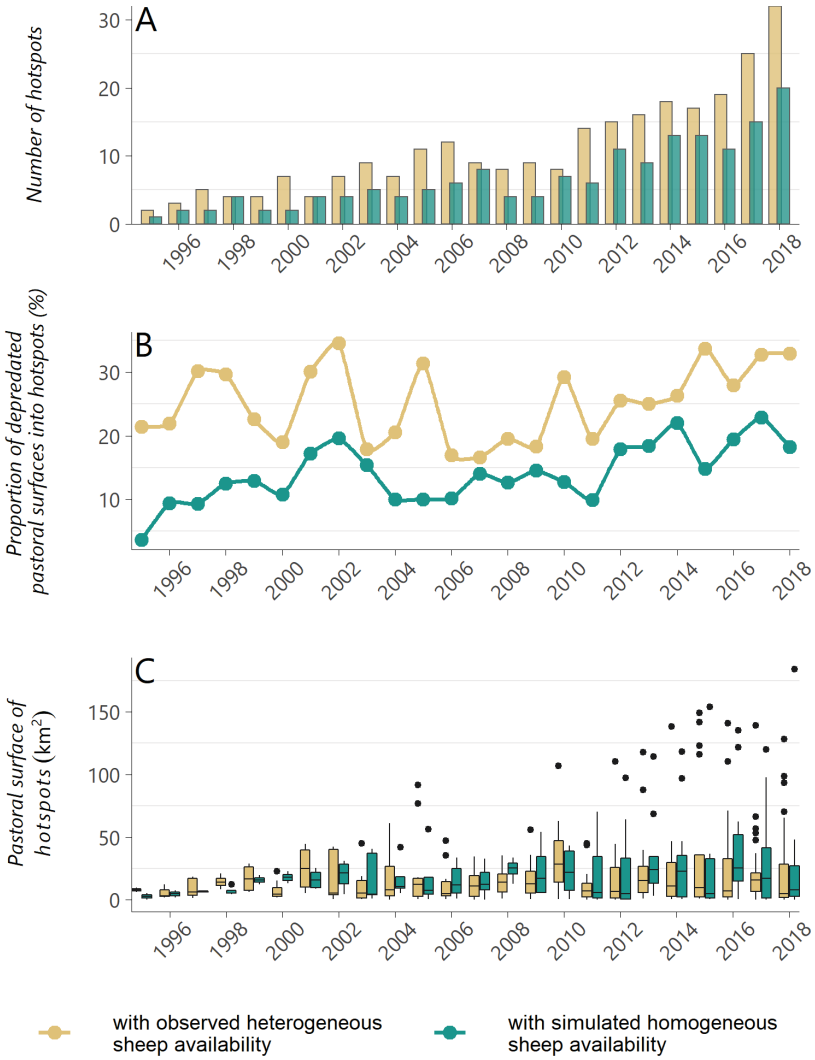


Figure 4.7: Descriptive results of the Kulldorff statistic used with the observed heterogeneous (yellow) or simulated homogeneous (blue) sheep availability, for each year, within the study area. (A) Number of significant hotspots; (B) Proportion of depredated pastoral surfaces into significant hotspots in the whole set of depredated pastoral surfaces; (C) Distribution of the sum of the areas of the pastoral surfaces of each hotspot (with outliers as black dots). Credits: O. Grente

The *Kulldorff* statistic showed in AURA-PACA...

- an increasing number of hotspots,
- that were recurrent in the MNP and in the south,
- and that could be particularly large since 2013,
- but the statistic identified more hotspots when adjusting for sheep risk exposure,
- especially hotspots encompassing small flock sizes or low grazing times, which would have remained undetected if the sheep risk exposure was not taken into account.

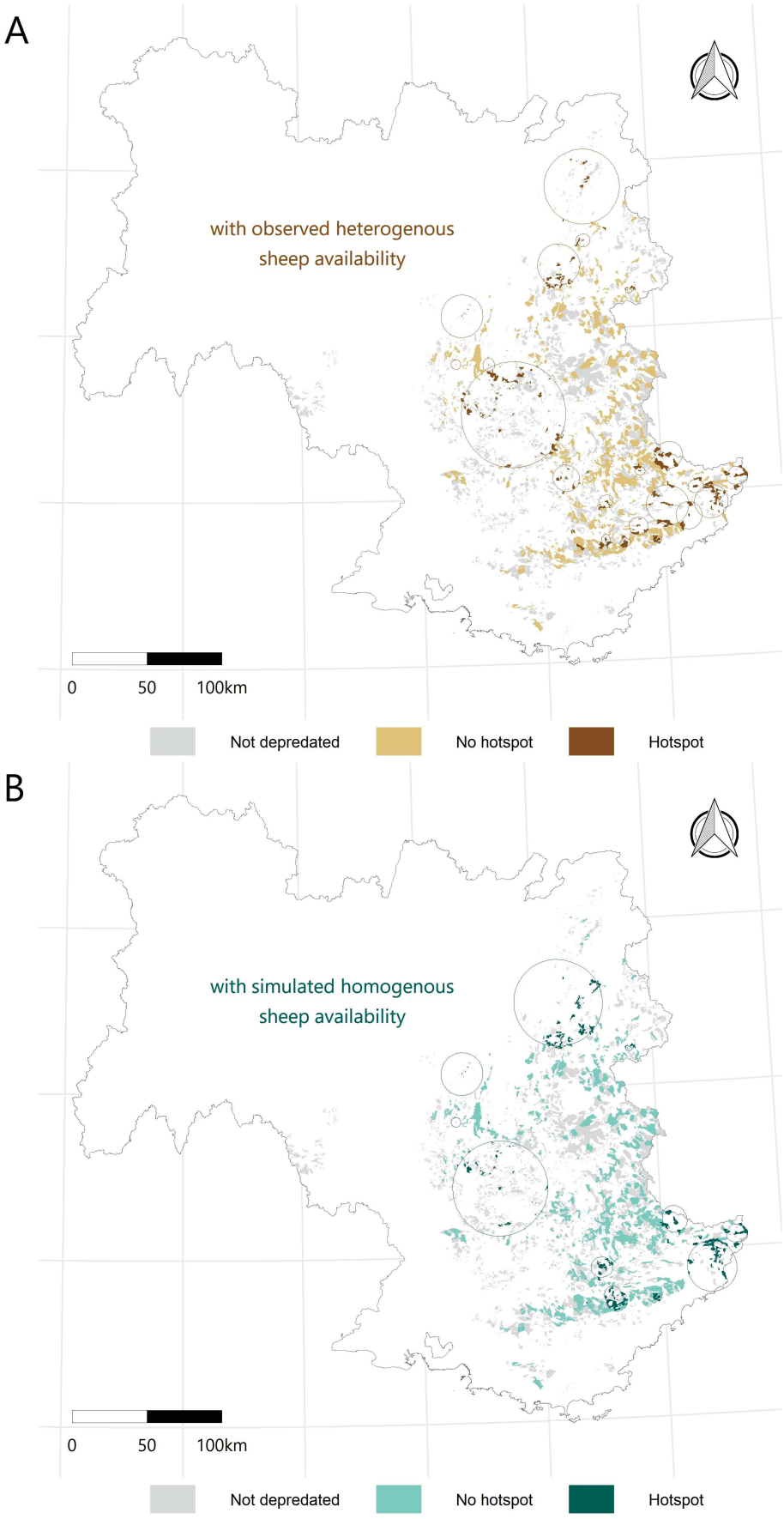


Figure 4.8: Locations of depredated pastoral surfaces identified as hotspots (dark colour) or not (light colour) in the study area in 2017 according to the Kulldorff statistic results adjusted for the observed heterogeneous (A) or simulated homogeneous (B) sheep availability. Pastoral surfaces within the same circles belonged to the same hotspot. Pastoral surfaces which were not depredated (grey) were shown for information but were not used in the statistical analysis. Results for all years are available in the interactive version at https://oksanagrente.shinyapps.io/Hotspots-SuppFig5/ (Figure D.5). Credits: O. Grente

4.6 Discussion

Reliable estimates of hotspot locations can inform risk models [268] but also provide a full-fledged management tool. Year-to-year analysis of hotspot identification allows the localisation of long-lasting hotspots which generate conflicts [274]. Once the hotspots are identified, the causes favouring depredations can be investigated in these areas. The involved farmers can be helped in the implementation of appropriate preventive tools, such as fencing or guardian animals [284]. Therefore, reliable estimates of hotspot locations are a powerful tool for allocation of conservation resources, especially in areas newly recolonised by large predators as in Europe or in North America.

[284]: Littlewood et al. (2020), *Terrestrial Mammal Conservation: Global Evidence for the Effects of Interventions for Terrestrial Mammals Excluding Bats and Primates*

Depredation hotspot analysis can however be of limited interest if the analysis is not adjusted for livestock availability. Depredations primarily rely on the rate of encounters between predators and livestock [31]. Therefore, the clustering of depredations is generally a primary representation of livestock clustering. However, other factors can favour depredations, such as environmental, husbandry or predator-linked factors, on which managers can attempt to act to decrease depredations [284]. If the hotspot analysis does not adjust for the underlying livestock distribution, the distinction between hotspots caused by the primary livestock risk exposure and the hotspots caused by other factors cannot be easily assessed. Moreover, pastures encompassing low depredation levels but with low flock exposure can remain undetected hotspots when the analysis is not adjusting for livestock availability. The consequences of depredations for the involved farmers are yet high in these situations because a high proportion of the flock is lost to predation [274]. Adjusting for sheep availability in the *Kulldorff* analysis allowed us to detect pastoral surfaces within hotspots with low sheep counts and grazing time. Similarly, adjustment for the underlying population at risk is also crucial in epidemiology. Without population adjustment, the densely populated areas would generally be identified as hotspots because of their high rates of cases, whereas less dense areas would not, despite disease rates higher than expected under randomness when considering the amount of population [285].

[285]: Diggle et al. (2007), 'Second-Order Analysis of Inhomogeneous Spatial Point Processes Using Case-Control Data'

When looking at the summarised depredation pattern through K_{inhom}, results also differed according to the adjustment for sheep availability, for sheep distribution only or neither of the two types of information. The typical clustered pattern (*i.e.* aggregation followed by repulsion [268]) was observable for 11 years over 24 years when adjusting for sheep availability in the analysis, against 2 years when adjusting for sheep distribution only and was not observed when neither of the two types of information were integrated. This difficulty to detect a clustered pattern when omitting livestock availability can prevent the investigation on the spatial scales of the depredation process, whereas it can help managers to understand the depredation mechanisms. For example, the K_{inhom} analysis allowed us to investigate if the depredation process could be explained by wolf territoriality. Buffer zones can indeed emerge between wolf territories, that wolves tend to avoid because of intraspecific strife risks, resulting in a localised lower risk of predation [226]. The hotspot radiuses were estimated between 12 and 50 km in our K_{inhom} analysis at the local and regional scales, which did not match with the

[226]: Mech (1977), 'Wolf-Pack Buffer Zones as Prey Reservoirs'

7–8 km wolf territory radius estimated in France through telemetry and genetic tracking [115]. Therefore, these results suggested that, if wolf territoriality shaped the depredation process, it was not the only factor and environmental features or husbandry practices should also be investigated.

The variation in the depredation pattern and in the hotspot locations across time can also help managers to evaluate the effectiveness of conservation actions. In this study, the K_{inhom} analysis showed a tendency of the depredation process to clustering (aggregation followed by repulsion) from 2004, and then showed a to randomisation from 2012, at the regional scale. On the other hand, the adjusted *Kulldorff* analysis showed a higher proportion of depredated pastoral surfaces identified as hotspots in the last years of the study period. Put together, these results suggested that the depredation hotspots tended to form large, almost continuous zones where the high depredation rate was homogeneously distributed in the last years of the study period. This randomisation pattern did not seem to be linked to the increase of the area recolonised by wolves, as the randomisation occurred at the local scale long after wolves recolonised the MNP. The depredation risk homogenisation among pastoral surfaces could result from the increasing number of farmers who protected their flocks against wolf depredations during wolf recolonisation [113], as suggested by [71]. [71] studied the trend of wolf depredations in the same regions of France as ours, and found an equivalent time slicing as ours: depredation levels stabilised between 2005 and 2009, and increased between 2010 and 2017, where we found a tendency to clustering between 2004 and 2012, and to randomisation between 2013 and 2018. [71] suggested the beginning of the implementation of protective measures between 2005 and 2009 could have stabilised the depredations in unprotected pastures only, but protection generalisation between 2010 and 2017 could have extended the depredation risk to the protected pastures, therefore explaining the positive trend of depredations.

[113]: MTES et al. (2018), *État des lieux et diagnostic de la situation dans la perspective de la rédaction du futur plan national d'actions 2018-2023 sur le loup et les activités d'élevage*

[71]: Meuret et al. (2021), 'Missing Shots: Has the Possibility of Shooting Wolves Been Lacking for 20 Years in France's Livestock Protection Measures?'

In addition, our methodology detected more hotspots that encompassed a few numbers of pastures (with small total sheep counts and low total grazing time) compared to the analysis not adjusted for sheep risk exposure. Contrary to the large and persisting hotspots detected in the MNP and in the south of the French Alpine Arc, these hotspots could be sporadic. This could result from brief conditions favouring depredations (*e.g.* failure in protective measures). If, however, they were not sporadic, their non-detection with the current hotspot identification used in France could cause emerging hotspots that would remain not detected by authorities.

For both the K_{inhom} and the *Kulldorff* analyses, information about livestock availability was of paramount importance to detect the depredation pattern and hotspot locations. This information is usually hard to obtain, even more at a regional scale. This explains why the studies on depredation hotspots generally did not adjust for livestock information (*e.g.* [268]) or only for livestock distribution (*e.g.* [269]). Here, our information on livestock availability was limited in time to two censuses which in total covered a period of 5 years. Limiting our study period to this 5-year period would have been possible and still informative to show the discrepancies in the results of the K_{inhom} and of the *Kulldorff* analysis when adjusting or not for livestock availability. This being said, the extension of

the use of livestock information to years surrounding the census' periods, in the context where pastoralism is a traditional activity with limited fluctuations in pasture usage, brought valuable information about the dynamics of the depredation pattern.

Our methodology enables the detection of hotspots, where depredations abnormally cluster, and can help management of depredations. However, managers should not overlook areas where depredations exceed a certain tolerance threshold even when livestock availability explains the depredation level. These areas, which are not detected as hotspots, can still generate resentment from farmers towards wolves and undermine conservation efforts. Moreover, managers should remain careful concerning the parameterisation, especially the limit size of zones Z in the *Kulldorff* analysis which can substantially modify the spatial extent of hotspots.

4.7 Conclusion

Chapter 4: Hotspots of depredation

After a period of clusterisation of depredations up to 2012, the depredation pattern tended to homogenise in the last years, in the French Alpine Arc. It could be due to the ongoing standardisation of livestock protection, producing an homogenisation of depredation risk over large areas of similar environmental characteristics.

Our results showed that the annual clustering analyses adjusted for livestock availability could fill the current gaps in the methodology used by the French authorities, through *1)* a smaller spatial analysis scale and *2)* the detection of hotspots at the annual scale without relying on previous years, therefore allowing for detection of emergent hotspots, even when they are encompassing small areas. These analyses require a good level of information, which is however available for the French Alpine Arc.

We encourage the use of these adjusted statistical analyses for any context of large predator conservation and management of depredations. Contrary to the conventional wisdom which relegates clustering analyses to a preliminary step in risk modelling, the estimation of hotspot locations is a full-fledged decision-making tool. Hotspots are the first targets for allocation of conservation resources, or for investigation *in situ* of the causes favouring depredation. The livestock owners in hotspots can be helped, financially or technically, to quickly adapt their husbandry practices according to the pastures they use and the predator they face.

Using spatial statistical analyses such as the K_{inhom} or the *Kulldorff* analyses combined with livestock availability data would substantially improve the reliability of the estimates of depredation pattern and of hotspot locations, and therefore their use of for conservation. Finally, the variation in the estimated depredation pattern or in the hotspot estimates are valuable conservation indicators to evaluate the level of conflicts between livestock owners and large predators, as well as the effectiveness of the conservation tools applied to reduce depredation levels.

Discussion

5 Discussion

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Understanding the depredation in grey wolves (*Canis lupus*) and its interactions with lethal measures in France proved to be a difficult exercise, but more than that, a highly stimulating study.

I will first discuss in section *Draw away from polemic* the polemic inextricably linked to the subject of this thesis. I will explain how I acknowledged this debate but attempted at the same time to take a step back in order to conduct my studies as objectively as possible. I will also explain why I gave the highlight to the transparent communication of my results, but also of the current knowledge.

I will then discuss in section *Synthesis of the results* the results of the thesis. I will highlight the most important of them, and the new information they provide regarding the current scientific literature. I will also explain the limits of the thesis studies and the biases involved by the analysed data.

Finally, I will end the discussion in section *What comes next?* by drawing the potential perspectives of my results on the current and future management of depredations of wolves in France, and what could be the next moves for scientists on the subject.

5.1 Draw away from polemic

What the thesis studied, what it did not

The subject of lethal control of wolves is laden with history, and is also anchored with our present. It reveals how much the paradigm of our relationship with large predators changed through modern time and is still changing today. The subject is now entwined with our contemporary challenges to slow down the rate of biodiversity loss and to choose sustainable agricultural systems. Sometimes, both challenges go hand in hand. Sometimes, they intertwine, as in the case of predation of wolves on livestock, notably the livestock raised by pastoralism.

States have to solve the dilemma of these conflicting priorities. As in many countries facing the depredation by large predators, the French government has chosen to reconcile these challenges and to promote *coexistence* between farmers, their grazing livestock and the wolves [77]. But coexistence generally implies compromises from both sides. At this stage, debate can already be raised concerning this choice. Which, from the wolf or pastoralism, is the most positive for the environment and for us? Should a priority prevail on the other?

This debate can rely on the work of scientists who study the effects of wolves (*e.g.* [286]) or of pastoralism (*e.g.* [287]) on the natural environment. My work had not the objective to study these effects. I adopted the governmental position that both wolves and pastoralism exist and share the same space in France, and that the goal of conservation is the

[77]: MTES et al. (2018), *Plan National d'Actions 2018-2023 sur le loup et les activités d'élevage*

[286]: Martin et al. (2020), 'Deer, Wolves, and People: Costs, Benefits and Challenges of Living Together'

[287]: Homewood et al. (1984), 'Pastoralism and Conservation'

upholding of both. In other words, **my work did not question the pros and cons of wolves or of pastoralism, or if coexistence is the right path**.

Among the management tools to promote coexistence between wolves and grazing livestock, France authorised lethal measures, more precisely 'defence culling' and 'harvesting'. The high controversy about this tool emerges from ethics and uncertainty about its effects on wolf populations and its efficiency to reduce the depredation levels, whether it is in France or abroad [133]. This scientific uncertainty fuels the debate, with sides emerging in favour or in disfavour of the use of lethal removals, including amongst French scientists, where some take openly position in favour of their use (*e.g.* [71]) when other express doubts and concerns about it (*e.g.* [288]), both sides agreeing with the choice of coexistence.

[133]: Treves et al. (2019), 'Predator Control Needs a Standard of Unbiased Randomized Experiments With Cross-Over Design'

[71]: Meuret et al. (2021), 'Missing Shots: Has the Possibility of Shooting Wolves Been Lacking for 20 Years in France's Livestock Protection Measures?'

[288]: Benhammou (2018), 'Tribune. Nouveau Plan Loup : Déception et Inefficacité.'

My work consisted in reducing the uncertainty about the effects of lethal measures on the recorded successful depredations, by focusing on the French case of their application. I did not study the effects of lethal measures on the perception of the damages by livestock owners or on the social acceptance of wolves. I also did not study the ethics of lethal measures. These are other study approaches of lethal measures, of which the results can be disconnected from the effect of lethal measures on the depredation levels. If you are interested by these approaches, I refer you to [90], [289] or [290] to name but a few.

[90]: Shivik (2006), 'Tools for the Edge: What's New for Conserving Carnivores'

[289]: Scasta et al. (2017), 'Rancher-Reported Efficacy of Lethal and Non-Lethal Livestock Predation Mitigation Strategies for a Suite of Carnivores'

[290]: Epstein (2017), 'Killing Wolves to Save Them?'

I had at my disposal the data provided by the French administration related to *a)* depredations since the beginning of wolf's recolonisation of France in the nineties, *b)* all wolves killed by legal culling since 2011 and *c)* the wolf's national monitoring. Data on known poaching was too scarce to be included in this work, and data on non-lethal deterrent shooting (*i.e.* in the air), as well as all data related to the implementation of non-lethal measures, as livestock guarding dogs, was non-existent.

The available data allowed the analysis of the effects of culling on the depredation levels, but not on the wolf's population detailed structure and dynamic. Because data were administrative and not part of a scientific protocol, the highest scientific standard (the '*gold*' standard [133] [132]) was impossible to reach. I attempted to fill the methodological gaps as best as I could regarding the available data, in order to provide the most reliable and interesting results possible. This analysis was presented in Chapter 3 (Effects of culling on depredation).

[132]: Treves et al. (2016), 'Predator Control Should Not Be a Shot in the Dark'

Hence, **the available data did not allow the analysis of the big picture *i.e.* the effect of culling on the wolf's population structure and dynamic and the repercussions of this effect on the depredation phenomenon**. It was therefore impossible to conclude with certitude on the mechanisms with which the removals could or could not change depredation's levels in France, for example through population size reduction or pack dissolution. No published study across the world used this integrated approach to analyse the big picture of lethal removals of wolves. Because the polemic relies on the uncertainty concerning the big picture of the lethal removals, my collaborators and I proposed an integrated model to explore it. Modelling something as complex as wolf population and wolf depredation behaviour was ambitious. Our model is full of approximations, and is not intended to be strictly speaking a management tool. I nonetheless hope it will help to see clearer about the

whole dynamic related to lethal control and that it will help to trigger future field experiments on the subject. This integrated analysis was presenting in Chapter 1 (The wolf population dynamic) and Chapter 2 (The depredation behaviour). I placed them before Chapter 3 in the thesis because I thought it was important to catch the big picture before going into the analysis with the French observed data, that was restricted to a part of the subject only.

Transparency

I believe the essential part of the polemic on lethal removal does not only comes from a lack of scientific knowledge, but also from misinformation, notably by **talks turning our incertitudes into certitudes**, whether it is voluntary or not. In this thesis, I insisted in documenting every beginning of chapter with the related current scientific knowledge. The goal was to ensure that the readers and I had the same common ground of knowledge before going deeper in the analysis.

In the introduction of the thesis, I decided to make a description of the context of management of depredations in other countries of Europe or in the USA. Because the situation in France is generally compared to these countries, and because most of the scientific literature comes from outside of France for this subject, **I believed that it was essential for readers to be able to replace each result from a given study within its context, in order to avoid the risks of generalisation**. Too often, extrapolation has been made on this subject without taking precautions, including by informed people or scientists. I will give you two concrete examples which occurred during the preparation of the thesis.

First, a report[1] [291] by Michel Revelin introduced himself as a territorial engineer, was circulated by the pastoral protection association *Cercle 12* to the pastoral stakeholders of *Groupe National Loup*[2] (J. Steinmetz, *pers. com.*). Besides the fact that the author openly called the coexistence into question, he also reviewed the scientific literature on the subject of lethal removals of wolves. He notably reviewed or rather quoted large parts of the study of [248] in France. According to him, this study demonstrated that the culling is efficient to reduce depredations in France. What he omitted to mention is that this study was not peer-reviewed by the scientific community. When addressing to a large public, it is necessary to mention that a Master thesis, as interesting as it is, has not the same scientific validity than a published and peer-reviewed article. For example, he quoted from [248]: '*the defence culling and the harvesting significantly decrease the number of attacks*'. As said in the literature review of Chapter 3, [248] analysed 195 *decrees* for defence culling and 15 *decrees* for harvest: in total, it corresponded to the deaths of 4 wolves. Therefore, [248] should have rather wrote: 'the *decrees of* defence culling and of harvesting significantly decrease the number of attacks'. Indeed, her results showed that it was the authorisations of legal culling that significantly reduced the levels of attacks, but not the deaths of wolves themselves (only 2% of the analysed decrees). A good peer-review of her work would have made her correct this sentence to avoid this kind of approximations, leading to risks of misinterpretations as Michel Revelin made. Finally, he concluded his report, p.51, by '*To fight against depredation, interventions on entire packs related to depredation appears as logical and the most efficient strategy* [to adopt

1: Available online here.

[291]: Revelin (2019), *La Question Controversée de La Dynamisation de La Reproduction Des Loups Par Les Tirs Létaux. Ses Conséquences Supposées Sur l'accroissement de La Prédation Sur Le Bétail.*

2: *Groupe National Loup* is a group representing all stakeholders (public or private), concerned by the management of wolves for depredations in France. The group is created by the prefect in charge of the implementation of the wolf depredation management plan in France. The group represents the official meeting place of all stakeholders of this subject in the country [292].

[248]: Le Cam (2012), *Evaluation de l'efficacité de la mise en place de tirs de défense ou de prélèvement sur les attaques des troupeaux domestiques par le loup Canis lupus*

in France], *as confirmed by the study of* [96]'. No precautions here were made on the fact that the study of [96] was conducted in the Northern Rocky Mountains in the USA, where the pastoral, environmental or wolf density contexts were different from the French Alpine Arc, and that what could be efficient in the USA could not be efficient in France.

[96]: Bradley et al. (2015), 'Effects of Wolf Removal on Livestock Depredation Recurrence and Wolf Recovery in Montana, Idaho, and Wyoming'

The second concrete example is the televised interview[3] of the scientist Dr. Pierre Jouventin, who is a former researcher at the laboratory CEFE (where I conducted my PhD thesis), in the journal emission *28 minutes* broadcasted by the French-German TV channel *Arte* [293]. He said '*This has been demonstrated in American studies [...:] when you shoot, you explode the pack, and from that moment the formerly psychologically castrated wolves can reproduce and they attack sheep because they do not have the hunting techniques on wild animals which are more complex. [...] [Therefore, culling of wolves] does not work, we have to change the method [in France].*' I believe he made reference to the study of [174], but he did not mention that 1) pack dissolution is a risk (not an absolute result), 2) this risk was associated with a breeder's death only, 3) there is no scientific consensus about the fact that dispersers attack or eat more domestic preys than wolves in pack, and 4) what could be true in the USA could not be true in France. He also added that the cohabitation between wolves and livestock in Spain and in Italy '*goes really well*'. Yet there was an average of 2 951 livestock recognised as killed by wolves per year for the period 2003–2010 in the sole region of Asturias in Spain. As for Italy, poaching was estimated to kill a proportion of wolves as high as the current legal culling in France, and poaching was '*tacitly accepted by public authorities*' [70]. I would say that precautions about the '*really well*' situations in Spain and in Italy claimed by Pierre Jouventin would not go amiss. The fault is also shared with media, as raised by Etienne Klein about the general relationship between research and media: *'If an honest researcher says* "I do not know" *on TV, he will not be invited again.'* [294].

3: Available on Youtube here.

[293]: Arte (2021), *Le loup, ce mal-aimé*

[174]: Brainerd et al. (2008), 'The Effects of Breeder Loss on Wolves'

[70]: Ciucci (2015), 'All's Well That Ends Well? Wolf Recovery and Conservation in Italy'

I believe this type of assured interventions from scientists or people with influence, where not enough mentions to uncertainty in research are made (or where false information are even spread), can wrongly orientate public opinions in one side or the other, can participate to the polarisation of the debate, and in turn can have a counter-productive impact on the choice of management policy.

Given that this type of interventions is frequent on the inflamed subject of lethal removals of wolves, I attempted to be as most transparent as possible. My first objective was to sweep away the preconceptions that readers could have on wolves, on depredations or on their management, in one way or the other. My second objective was to settle a trusting relationship with the readers by demonstrating that I conducted my work as objectively as possible.

As said previously, these two objectives could only be reached by a presentation of the knowledge that the scientific community has and has not, and the associated contexts, for each thesis chapter. But transparency is also a matter of communication. Because a thesis can be tough and exhausting to read, I also tried to facilitate the reading through an interactive document (for the electronic version), the use of green boxes to synthesise the key messages of important sections, and the use of

margins to insert comments helping the reader to understand technical parts or to get an immediate insight of the cited references.

Still with this aim to facilitate the communication of the thesis results, I developed interactive applications for Chapter 4: maps of the analysed data and maps of the statistically identified hotspots are available online (see Appendix D). I hope this will help readers and potentially managers in France and elsewhere to more easily grasp the results, their interests and their applications for the management of depredations. For the scientists, I intend to provide the codes of the analyses on my github once the studies will have been peer-reviewed and published.

My supervisors, collaborators and I also made the choice to release, at the middle of the thesis preparation, an article explaining the aims of the thesis, the gaps in the literature review and the methods that we intended to use [295]. This article is not peer-reviewed by the scientific community and had the only aim to communicate about the thesis to the French public and to other scientists. The article is available in Appendix E. It has been published in *Faune Sauvage*, a journal edited by the Office National de la Chasse et de la Faune Sauvage (replaced by the new establishment Office Français de la Biodiversité since 2020).

[295]: Grente et al. (2020), 'Tirs dérogatoires de loups en France : état des connaissances et des enjeux pour la gestion des attaques aux troupeaux'

I am also preparing an interactive web page in French about Chapter 3 where the raw data will be presented through interactive maps or tables, but also the main sections of methods, and all the results through a user-friendly interface. This page is prepared with RMarkDown and codes will also be accessible. I also plan to translate the whole thesis in French instead of only providing a translated summary.

I hope that all these choices of transparency will improve the communication and visibility of my research and help managers in France or elsewhere. What seems to me the most important is that I hope the thesis reflects the objectivity of my studies that I tried to respect as best as I could.

5.2 Synthesis of the results

I answered to the question *are lethal measures efficient to reduce depredation levels in France?* through two approaches.

The first approach was to understand how the effects of the lethal measures on the wolf population structure and dynamic could modify the depredation levels in return on the long term.

The second approach was to exclude from the analysis the changes on the wolf population provoked by lethal measures, and to study only the effects of lethal measures on the depredation levels.

I also added two more questions to the thesis. The first one was related to the understanding of the depredation spatial pattern: *do depredations cluster and if so, on which distance and does this pattern change over the years?* The second one was related to the management of hotspots: *how can we possibly identify depredation hotspots in France by taking into consideration the spatio-temporal livestock distribution?*

What have we done new?

The Individual Based Model

The first approach to study the efficiency of lethal measures consisted in **modelling** altogether the three following components: the lethal removals, the grey wolf population and the depredations.

We chose this integrated modelling approach[4] where a system is fully simulated instead of analysing observed data in France. The reason for this choice is double. First, the available data about the grey wolf population structure in France included too many unknowns. For example, the identity of breeders within packs was unknown, pack turnover was hard to attest and to date, and therefore made it difficult to explore the impacts of lethal removals on depredation through pack dissolution (Assumption 2). Second, even if the data were available, the simultaneous analysis of three spatio-temporal datasets (about removals, wolves and depredations) would be methodologically very challenging at the scale of the French Alpine Arc. Modelling allowed us to remove the unknowns and to simplify the analysis.

4: This approach is also called *in silico*

Analysing all the interactions between removals, wolves and depredations through observed data has never been done. Except [186], the modelling integrated approach for this subject has never been applied either. In [186], the model intended to provide clues about the right management approach between preventive, reactive and population-size managements. It did not explore the population mechanisms as pack dissolution or the variations in the depredation behaviour, which are hard to decrypt.

[186]: Haight et al. (2002), 'Computer Simulation of Wolf-Removal Strategies for Animal Damage Control'

We modelled each component one by one:

1. **The grey wolf population**, modelled in Chapter 1. We integrated most of the grey wolf population mechanisms. Besides the mechanisms already found in models on wolf population, we integrated 4 more: pack dissolution, adoption, budding and sex-biased replacement of missing breeders. These mechanisms could impact wolf population dynamic and structure, which in turn could impact the individual depredation behaviour of wolves.
    - We tested different configurations for these 4 mechanisms in Chapter 1.
    - We only retained the most likely configurations for these 4 mechanisms in the final model (*i.e.* the entire loop of removals, wolf and depredations).
2. **The depredation behaviour**, modelled in Chapter 2. After a thorough review of the depredation behaviour in wolves, we decided to model the depredation risks for each individual in function of its pack food needs and in function of three tested characteristics: (1) the hunting efficiency according to the wolf's age or the composition of its pack, (2) the abilities of individuals and packs to learn to bypass protection measures or (3) their abilities to better exploit the wild resources of a territory as time flows by. The first hypothesis has been the object of previous studies (but never analysed in relation to lethal removals), and the second and third hypotheses were only assumptions from literature or field observations, and have never been formally tested.

3. **The lethal removals**, modelled in Chapter 2. We decided to model the two types of culling applied in France: the defence culling (selective) and the harvest (not selective).

Then, the model was launched with the three components. The model acted as a free system. I think this is **the force of the model: we have modelled each component separately, but we minimised our arbitrary print on the interactions between these components**. For example, we did not directly code for lethal removals to dissolve packs. This phenomenon only arrived when breeders were killed, whether it is by lethal removals or not, to reflect the observations made by [174].

The kernel method

The second approach to study the efficiency of lethal measures consisted in **analysing** the effects of lethal measures on the distribution of depredations in space and in time with the observed data in France.

This analysis was simplified compared to the first modelling approach, as the changes the lethal measures could have on wolf population were not studied. Consequently, this approach was not mechanistic but empirical: we did not try to understand the inner workings of the effects of lethal control. We only put in relation the lethal removals and the depredations. This analysis was presented in Chapter 3.

This empirical approach had already been done several times by previous studies, including for the grey wolf. However, any analysis had ever combined the three following methods:

1. A comparison of the depredation levels before and after the removals, in the spatial vicinity of removals,
2. An explicit consideration of the seasonal dynamic of depredations in space and time,
3. A continuous spatial and temporal gradients around the removal events.

Up to now, most studies had analysed the relationship between removals and depredations through correlations, whereas this methodology prevents to correctly identify the cause and the effect (see section *Literature review* in Chapter 3) and must therefore be avoided.

For the rest of the previous studies, they chose to compare depredation recurrence rates according to the management response used after each depredation (*e.g.* removal or no removal). They involved inter-site comparisons where the risk for confounding factors was higher than in a before-after comparison as we chose. These studies did not use an explicit use of the livestock distribution in space and time and a continuous spatial and temporal gradients. Moreover, their number of analysed depredations (923 in [97], 967 in [96], $\leqslant$ 200 in [52]) was greatly lower than in our study (7 747 depredation events). The number of killed wolves was however generally higher in these studies (1 440 in [97], $\sim$ 1 000 in [96]) than in ours (236), but their methodology did not explicitly use this data for the analysis of the lethal removal effects: they only used the type of management response.

[97]: Harper et al. (2008), 'Effectiveness of Lethal, Directed Wolf-Depredation Control in Minnesota'

[96]: Bradley et al. (2015), 'Effects of Wolf Removal on Livestock Depredation Recurrence and Wolf Recovery in Montana, Idaho, and Wyoming'

[52]: Santiago-Avila et al. (2018), 'Killing Wolves to Prevent Predation on Livestock May Protect One Farm but Harm Neighbors'

Moreover, only one published study about the effect of lethal measures on depredation due to wolves analysed European data [67]. This study used a correlational approach. All the others have only focused on data from North America (essentially the contiguous USA). When including non-peer-reviewed reports, only [248] used French data, but she used decrees and not removals, and did not use a continuous spatial and temporal gradient around the decree events. Despite this, the methodology she used was the closest to ours. Thus, there was a gap in the scientific literature about the effects of lethal removals in France or in a similar context.

[67]: Fernández-Gil et al. (2016), 'Conflict Misleads Large Carnivore Management and Conservation'

[248]: Le Cam (2012), *Evaluation de l'efficacité de la mise en place de tirs de défense ou de prélèvement sur les attaques des troupeaux domestiques par le loup Canis lupus*

To summarise, **the methodology I applied minimised as best as possible the risk for confounding factors given the provided data**. Moreover, the output of the results also allowed for **compiling the effects of lethal removals at all spatial and temporal analysed scales in one graph only**. I believe this facilitated the understanding and communication of the results.

The depredation spatial pattern and depredation hotspots

I studied the depredation spatial pattern in France and identified the depredation hotspots through spatial statistical analyses. The analyses were presented in Chapter 4.

The high number of recorded depredations in France (18 764 from 1995 to 2018) made the use of spatial statistical analyses very relevant to study the depredation pattern. To my knowledge, no study has attempted to analyse the summarised spatial structure of depredations (*i.e.* the range of distances over which the pattern generally exhibits clustering, randomness or regularity [257]), whether it is for wolves or another predator. This analysis is yet interesting to investigate the relation between the summarised spatial structure of depredations and the summarised spatial structure of the predator population. In the case of grey wolves, this allowed me **to investigate if the depredation process could be explained by wolf territoriality**.

Concerning the identification of hotspots, spatial statistical analyses have already been used in previous studies, but have never been corrected for the unequal exposure of sheep flocks to depredation. Livestock exposure to depredation depends on the flock sizes, the grazed area but also the time spent on the pastures. The spatial pattern of depredation is inherent to the livestock risk exposure. If livestock risk exposure is ignored, it is difficult to disentangle the hotspots based on high levels of livestock risk exposure from those where livestock risk exposure is low but where predation rates are despite that disproportionally high.

This is problematic for management of depredations. In France, the priority for conservation subsidies is made on *cercles 0*, which are the hotspots defined according to the number of depredations within municipalities. Focusing on municipalities may not be the most relevant spatial units because it can introduce biases relative to the sizes of municipalities: the small municipalities, which encompasses generally less pastoral surfaces and less depredations, are less likely to be identified as hotspots. It is therefore important for management to define hotspots with smaller spatial units (the pastoral surfaces) but also to take into account the size

of flocks and the grazing time, in order to identify flocks with unexpected high depredation levels. The **methodology I presented in this thesis allows for improving the identification of depredation hotspots for managers**.

What have we learned new?

The Individual Based Model

The main results of the complete IBM in Chapter 2 can be summarised within Table 5.1.

Table 5.1: The summarised results of the complete IBM. Results are presented through the hunting efficiency hypothesis and its three associated contexts which define livestock vulnerability according to wild prey vulnerability (row '*Livestock vulnerability*'). The types of individuals with higher depredation risks are different according to the context (row '*Higher depredation risks*'). Results of the culling effect (row '*Culling effects*') are summarised for both the individual level ('ind. level') and the individual and pack levels combined ('ind. and pack level'). The '*Responsible mechanisms*' were the biological wolf processes that were responsible for the effect of lethal removal on depredation. The '*Side effects*' were the biological wolf processes affected by lethal removals but without consequence on depredation. The verified assumption corresponded to the two assumptions mentioned in Introduction on page 24.

	Context 0	Context 1	Context 2
Livestock vulnerability	= Wild prey vulnerability	> Wild prey vulnerability	< Wild prey vulnerability
Higher depredation risks	Adults within packs (food needs)	Subadults (ind. level) or subadults, loners and dispersers (ind. and pack levels)	Adults (ind. level) or adults and wolves within packs (ind. and pack levels)
Culling effect	Depredation reduction	No change on depredation	Depredation reduction
Responsible mechanisms	Population reduction	No changes	Population reduction
Side effects	More pack turnover and lower disperser rate	Slightly lower disperser rate	More pack turnover and lower disperser rate
Verified assumption	Assumption 1	None	Assumption 1

Consequently, **our IBM supported Assumption 1 for two contexts of relative prey vulnerabilities. Thus, when livestock was less or equally vulnerable as wild prey, the lethal measures were efficient to reduce depredation through population reduction.** Pack turnover was more encountered for these contexts when culling was applied, but the social disruption of packs did not prevent culling to be effective in the reduction of depredation levels.

In the context where livestock is more vulnerable than wild prey, lethal measures did not change the depredation levels. This context was specific to Assumption 2 where individuals with lower hunting abilities (young or wolves alone) are thought to be the most likely to depredate. As mentioned in section *Interpretation of the results* in Chapter 2, the proportion of wolves killed under this context in our model was simply too low to show an effect in one side or the other. This was due to modelling choices, especially the fact to attribute negative depredation index to wolves the less likely to depredate under this scenario, instead of increasing the depredation index of those the most likely to depredate. Therefore, **we**

cannot conclude with certainty on the effects of modelled culling under context 1 where wolves with lower hunting abilities (young or wolves alone) were the most likely to depredate.

The kernel method

The analysis of the effects of lethal measures with the observed data in France should be divided into two main categories:

1. The analysis of the effects of the death of one wolf on depredation levels without distinction,
2. The analysis exploring the variability of the effects of these deaths according to the location, the date, the types of culling (defence or harvest) and the sex of the dead wolf.

The first general analysis indicated that the depredations were aggregated at a short distance of the locations of the culling events when conducting the analysis over 10 km. Depredations were found at a high quantity before and after the culling events. When pooling all culling events and correcting for pastoral use, culling events seemed unable to stop the depredations after their applications, but able to reduce the duration over which depredations occurred.

However, **the pooling of all culling events could mask highly variable results among culling events, resulting from different situations, notably according to locations and seasons**. These results are summarised within Table 5.2. The high variability in the results shows us that we have to be extremely careful when analysing all the culling events altogether without considering their characteristics.

Therefore, **I conclude that the effect of culling in France is highly variable according to contexts**, involving all types of results. The majority of the effects involved a reduction of depredations (10/25) or no change (8/25), and a minority indicated an increase of depredations (3/25)[5]. Spatial reports or spreads of depredations were suspected in 7/25 contexts and in 3/25 contexts, respectively. However, be careful about results in Table 5.2: they are very synthesised and if a context is of particular interest to you, you must check the corresponding kernel figure in section *Variability of the culling effects* in Chapter 3. **This table is not a substitution to the kernel figures**.

5: There were four cases with no clear result, annotated as '?' in Table 5.2, explaining the total of 25 here.

The depredation spatial pattern and hotspots

The analysis of the depredation spatial pattern revealed that the aggregation of depredations into hotspots was likely not explained by the unique factor of wolf territoriality and that other factors should contribute to the hotspot formation. Indeed, the average hotspot size encompassed several pack territories. Therefore, specific environmental conditions should also explain the aggregation of depredations at localised areas, such as in the Mercantour or in Canjuers.

As recolonisation by wolves progressed, the depredation pattern tended aggregate first, and then to homogenise in the French Alpine Arc. Depredations tended to uniformly spread over the French Alpine Arc, and the hotspots to concern larger and larger spatial areas as time went by.

Table 5.2: The summarised results of the kernel analysis of the effects of culling on depredation levels with data observed in France, when exploring the variability of the culling effects. '*Count*' indicates the number of analysed culling events associated with each group. The effect of culling on depredation levels is coded with ↘ (for a reduction of depredations), ∅ (for no effect), ↗ (for an increase of depredations) and ? for an unclear signal. **Intensity of the effect is not reported in the table**. The report of depredation refers to the possibility that depredations were still present after the culling events, but at another spatial zones compared to before the culling events. The spread of depredations refers to the possibility that depredations were still present after the culling events at the same locations as before these events, but also in other spatial zones. If reports or spreads are suspected, it is coded by ✓, if they are not, it is coded by ✗ and if it is not clear, it is coded by ?. All culling events corresponded to the death of one wolf only, which was independent from the other culling events, except for the 24 groups of interacting simultaneous culling events ('*Interacting, sim.*') and the 26 groups of interacting non-simultaneous culling events ('*Interacting, non-sim.*') in '*Culling combination*'.**This table is not a substitution to the kernel figures.**

Variable		Count	Effect	Report	Spread
Massif	Mercantour-Argentera	44	∅	✓	✗
	Préalpes d'Azur	33	?	✗	✗
	Trois Evêchés	18	↘	✓	✗
	Vanoise	18	∅	✗	✗
	Vercors	18	↗	✗	✓
	Préalpes de Digne	12	↘	✓	✗
	Ecrins	12	?	✓	✓
	Canjuers	11	?	✗	✗
	Cerces	10	↘	✓	✗
Altitude	Montane	136	↘	✗	✗
	Subalpine	75	∅	✗	✗
	Foothill	19	∅	✗	?
Wolf season	Autumn (Sep.–Oct.)	75	↘	✗	✗
	Rdv site (Jul.–Aug.)	72	∅	✗	✓
	Den (Apr.–Jun.)	43	↗	✗	✗
	Winter (Nov.–Jan.)	34	↗	?	✗
	Mating (Feb.–Mar.)	12	↘	✗	✗
Culled sex	Female	91	?	✓	✗
	Male	103	∅	✗	✗
Culling combination	Unique	236	∅	✗	✗
	Interacting, sim.	24	↘	✓	✗
	Interacting, non-sim.	26	↘	✗	✗
Culling type	Reinforced defence	95	∅	✗	✗
	Simple defence	78	↘	✗	✗
	Harvest	63	↘	✗	✗

This depredation homogenisation across the region could be due to the depredation risk homogenisation, potentially because of the number of flocks protected with the same set of protective measures increased over time. In the map of the '*cercles*' used by France to allocate non-lethal protective measure subsidies in 2020 (Figure 0.7), almost all municipalities in the French Alpine Arc region corresponded to *cercles* 0 and 1 which grant the same subsidies for the same non-lethal measures.

This general homogenisation tendency should however not shadow the presence of small hotspots, restricted sometimes to only one pastoral surface. Contrary to large hotspots, these small hotspots seemed to refer to one-time phenomenon, as they could appear only for one year only, without recurrence. **I hypothesise that small hotspots could reflect brief conditions, linked to weather, protection failures or specific individual wolves for example, whereas large hotspots could reflect lasting environmental conditions favouring depredations**.

For the whole study, whether it was for the summarised depredation spatial pattern or the identification of hotspots, the correction for flock sizes and flock grazing time was essential. The results were different when not considering these variables which primarily structure the depredation spatial pattern. In particular, hotspots encompassing few pastoral surfaces with small flocks or low grazing times were more likely to remain undetected when omitting livestock correction in the analyses.

What could be improved

Used data

The data collected about the French situation that we used, essentially in the kernel or hotspot analysis, included important biases that it is necessary to mention.

First, the data related to depredations were coming from the database *Géoloup*. This database is administrative. The collection of depredations is made in the context of depredation compensations, not for research. Therefore the needs for very precise location are low.

After discussions with Frédéric Bray (INRAE, *Maploup*), it appears that the geolocation of depredations within *Géoloup* can indeed lack precision. The spatial approximation would mostly concern depredations outside the context of *transhumance*, for example when depredations occurred in permanent pastures in hills or in plains. For these depredations, geolocation was randomly attributed within the hamlet, or if not known, within the municipality.

Most of the depredations analysed in the kernel and hotspot analyses were part of pastoral surfaces used for pastoralism. Therefore, the location bias should have a minimised impact in our analyses. However, the number of depredations outside these pastoral surfaces used is increasing with time (L. Garde, *pers. com.*). Therefore, if the methods I applied during my thesis were applied again in the coming years, this bias could become problematic.

Second, as mentioned in Chapter 4, the data related to pastoral surfaces corresponded to two censuses only, one in 1996–1997 and one in 2012–2014. At the scale of the French Alpine Arc, each census represented several thousands of pastoral surfaces and a great amount of work to get and to compile all this data. This explained why the censuses were limited in time. However, this limit included biases in our analyses because the pastoral use relative to each pastoral surface could have changed between years. This raises legitimate concerns for the construction of the pastoral correction for both the analyses of the culling effects and of the hotspots.

Missing data

Besides data that we had and that involved biases, there was also all the data that was unavailable for our analyses and that should have been included to investigate the culling effects or the depredation spatial pattern. I listed here the most important missing data. I ranged from the most realistically collectable data to the less.

Protective measures. I had no information about the implementations of protective measures. The only available information was the contract to governmental subsidies of the livestock owner of the flock concerned by a depredation in the *Géoloup* database. There was no information regarding the type of protective measures involved, let aside the implementation in the field. Moreover, it only concerned the flocks with reported attacks, not all flocks. This information was therefore unusable.

Wolf packs. The monitoring made by *Réseau Loup-Lynx* is mainly used for the estimation of wolf distribution and of national abundance. Because in the French Alpine Arc, almost all culling events occurred within the estimated pack territories, it was therefore pointless to explore the effect of pack presence on culling. I would have needed more precise information, for example the locations of *rendez-vous* sites or the pack sizes at the moment of the culling events. The identity of breeders was also unknown, at least for males; for females, breeding females concerned only 11.5% of culled subadult and adult females, which seemed quite low (13 culling events). The use of genetics have been considered and even investigated to identify the offspring-breeder relationship amongst the known genetic profiles. However, I was too short on time to explore this, and this would have also induce biases (*e.g.* which wolf is the breeder and the offspring between two related genetic profiles?).

Unsuccessful depredations. All my analyses with depredation data collected in France concerned depredations with dead livestock. [232] showed that the majority (70%) of attacks of flocks they watched in France ended in failure. Therefore, the depredation pressure is not linked to successful attacks only but also to unsuccessful attacks. The depredations I analysed could be a fair representation of all the attacks (successful or not): in other words, the most attacked flocks could be the most likely to have the highest rate of depredations. In this case, the analysed depredations would be a proxy for all attacks. Otherwise, they would not

[232]: Landry et al. (2020), 'Interactions between Livestock Guarding Dogs and Wolves in the Southern French Alps'

be a proxy and this could limit my analyses to successful depredations only. Because the IBM in the thesis is based on studies with generally access to successful attacks only[6], this also could also limit the results of the model.

6: or even with consummation only, which could not be a good proxy for predation as scavenging is frequent in wolves

Wild prey abundances and distributions. In the same way as the livestock abundance and distribution, depredations should also be dependent on the wild prey availability. This information in France was however unavailable to us at the scales required for the analysis of the culling effects.

Poaching. The available information relative to poaching was anecdotal (16/396 culling events). Poaching can have an effect on depredations that would be considered as '*noise*' here by statisticians. In other words, it would cause variations in the depredations that could not be explained by our dataset of legal culling. This limited the analysis capacity of the kernel method. However, poaching can be considered as part of the overall mortality that affect wolves and that remains unknown to us. In the IBM, poaching is part of the estimated '*natural*' mortality. Therefore, this limited the interference of poaching with our results. However, it did not annihilate biases. Indeed, poaching could be selective regarding the depredation behaviour of wolves (for example unreported defence shooting) and therefore poaching could not induce the same results as natural mortality.

Methods

There is not only the data which showed limits, but also the methods used for our studies.

Depredation hotspots. The identification of the depredation spatial pattern required the use of livestock abundances and of grazing times. This information was not available outside the pastoral context, for example in permanently pastured hills or plains. With the spatial expansion of depredations towards these areas, this could eventually cause problem. The same problem could appear if the method was applied in another area or region where the information about pastures is missing.

Modelling of the culling loop. The IBM could have been improved in many ways. I will only highlight the most important parts to improve. First, several mechanisms of the wolf population dynamic were set aside. I believe the incorporation of multiple breeding and the dependence of dispersal on pack density would have allowed the study of a saturated wolf population. The model of wolf population we developed in Chapter 1 is in fact more representative of a recolonising wolf population. This is less and less true for the population from the French Alpine Arc which shows signs of saturation.

Second, the modelling of context 1 should have been different in order to compare it to context 0 and 2. Instead of modelling adults with a -1 DI and subadults with a 0 DI, I should have modelled adults with a 0

DI and subadults with a 1 DI. Adults being prevalent in the population and culling impossible below 0, maybe this would not have produced more culling events compared to the current modelling of context 1, despite this modelling correction. A way to anticipate this would have been to increase the DI to 0.5 for adults, or to modify the lethal removal component.

To my knowledge, there is no study which showed that younger wolves were more likely to depredate than older wolves.Therefore, I could have focused only on the pack level of the hypothesis: the hypothesis that lone individuals are more likely to depredate than individuals in pack. In other words, it would have been better to allow, at least for the hunting efficiency hypothesis, the dissociation of the individual and pack levels. This is something I would like to correct before submitting the study to a journal.

The kernel method. I see three main limits in the method we used to detect the effects of culling on the depredation levels in France.

1. There is no investigation on the effects of culling on the number of dead livestock.

The kernel method was used with the depredation events regardless of the number of dead livestock involved in each depredation. Instead of using one point for one depredation event, I could have used as many points as dead sheep. However, I thought the number of dead sheep was less representative of the depredation pressure (constituted by successful but also failed attacks) than the depredation event. For example, I thought several successful depredation events of one dead sheep each could suggest a large number of general attempts of depredation from wolves. On the contrary, a large number of dead livestock in one depredation only would not necessarily suggest a large number of attempts. Nevertheless, I do not deny the interest to investigate the effects of culling on the number of dead livestock in studies to come.

2. The investigation of contexts is limited by the number of culling events.

Ideally, we would have combined the spatial and temporal groups to obtain the effects of culling in very specific contexts (*e.g.* in the massif Mercantour-Argenterra according to the wolf season). However, to be able to draw a reliable conclusion, the number of culling events that are included in a specific context must not be too low. In the available data, the number of culling events could sometimes be low according to the spatial or temporal contexts. Therefore, the count of culling events did not permit the combination of spatial and temporal groups of culling events.

3. The method did not provide a statistical significance of culling efficiency.

The analysis did not provide a statistical binary answer of significance: there was no *p-value* associated to the kernel figures. Therefore, our analysis did not provide a 'yes' or a 'no' answer regarding the efficiency of culling to reduce depredation levels.

I could have included statistical analyses of the depredation intensities provided by the kernel method. With Thomas Opitz and Olivier Gimenez, we actually worked on the development of models with the use of INLA (Integrated Nested Laplace Approximation). INLA is a method used to approximate Bayesian inference for example for spatio-temporal models. The model would have decomposed the kernel figure into pixels, with each pixel associated to a statistical value of significance **relatively to a depredation intensity control that would have been arbitrarily chosen by us**. However, there was not really one pixel that would have be the perfect representation of control. This control could have been chosen as the pixel right before the culling event and exactly at the culling location. However, this would have meant that all the depredation intensities on the long term before the culling event and farther from the event would not have been considered. Moreover, a statistical model requires a lot of data to increase its robustness: when dividing the culling events into groups of contexts, the model would have been less and less robust, whereas a signal could have still been observable through basic kernel method.

In addition, we thought the method was not only complicated to implement, but above all to explain to managers. **I believe it was essential for managers to grasp the methods and not only the results, in order to increase their trust in our results, and therefore to increase the chances that they could use these results during management.** This is why we decided to keep the methods as simple as possible, considering the spatio-temporal analysis it involved.

Another solution could have been to compute one value summarising the depredation intensity level before the culling events, and after (*e.g.* sums of all depredation intensities before or after the culling events). It would have allow a unique binary response to the efficiency of culling. However, I believe it was not the solution either, because it would have provided an oversimplification of the results: it was necessary to keep the information of depredation intensities relative to their occurrence in space and time. I believe it was important that the results showed that no unique binary answer could be provided to the question of the efficiency of culling events: **the depredation process occurs on large spatial and temporal scales and, in my opinion, cannot be summarised into one unique value, whether it is statistical or only mathematical**. It is true that the Table 5.2 provides a summarised unique trend for each context, however, it should only be seen as a guide to compare the results among contexts and to show the variations of the culling effects. I warned the reader that the kernel figures cannot be replaced with this table.

5.3 What comes next?

The necessary consideration of contexts

If by any chance managers in charge of wolf depredations have read my thesis, they could be highly confused about the use of culling. Is it efficient to reduce depredations or not? I know a binary answer would have greatly facilitated the choice to apply or not culling. However, because the process of depredations is complex, I am afraid the effects of culling would be

too. As [131] wrote about lethal removals of large predators, '*no single prescription will be appropriate for all conflict situations*'. In France, there is a multitude of conflict situations regarding wolf depredations.

[131]: Treves et al. (2005), 'Evaluating Lethal Control in the Management of Human–Wildlife Conflict'

I will nonetheless attempt to connect our results with potential applications. Our study on hotspots showed that depredations tended to form large recurrent hotspots that encompassed a group of pastures rather than isolated pastures. There could be a specific homogeneous dynamic of depredations within these areas. These areas could delimit management zones, where culling or other measures could be specifically adapted to these contexts.

An assessment of the situation for each hotspot could be realised. This assessment should not only be restricted to describe the pastoral practices, but should also be oriented to fill the gaps in our knowledge in the depredation behaviour too. This need is well summarised by [237], p.5:

> *One of the major factors that can modulate the efficiency of protection is the predator itself. Paradoxically, it is the less studied variable.*

[237]: Borelli et al. (2021), *Le loup dans le système pastoral. Rapport CanOvis IPRA-FJML 2013-2018.*

When [237] mentioned protection, they mostly referred to livestock guarding dogs. However, I think this statement could also apply to culling events.We still do not know if there are specific types of wolves which attempt and/or succeed depredations, notably regarding the context. At the end of Chapter 2 about the IBM, I mentioned the context of open pastures at high altitude and the more bushy closed pastures at lower altitude. There could be much more contexts than these two general ones.

A protection or an action such as culling that is efficient in one of these contexts could be inefficient in another one, because the involved depredation behaviour is not the same. This is the reason why we feel helpless regarding the culling effects. Even when this thesis provided clues regarding the relationship between culling and depredation in different contexts in Chapter 3, there was still something missing to fully interpret and understand these results: the wolf component. In this sense, the IBM, even if it was an academic exercise and not a tool for management, showed that changes in the depredation behaviour could modify the effects of culling.

From the kernel results, there are however some pieces of advice that can be provided regarding the application of culling. First, **there could be seasons that could be more appropriate than others to ensure that culling has the expected effects on depredations**. The culling events during the most cohesive periods for wolves (winter and den) were associated with an increase of depredations. Culling in these seasons could perhaps favour pack dissolution or multiple breeding. On the other hand, culling during periods of natural strong tensions (autumn and reproduction) led to a reduction of depredations without report or spread of depredation on adjacent pastures. This is consistent with findings from [254] who showed that there was a season of culling application more efficient than others[7].

[254]: Blejwas et al. (2002), 'The Effectiveness of Selective Removal of Breeding Coyotes in Reducing Sheep Predation'

7: However in their study, that was the pup-provisioning period (May–Aug.) that provided a reduction of depredations, when it would be associated with the den and *rendez-vous* site season in our study.

Second, there could be local contexts that would be more appropriate than others to ensure that culling has the expected effects on depredations. We have seen that culling in Préalpes de Digne or the massif of Trois-Evêchés was associated with a reduction of depredation, when it seemed

to induce spread, even increase of depredations in Vercors. However, when comparing contexts, we should not forget to also compare their depredation intensities, and not just the general effect. For example, the highest intensity in Vercors was 2.61 times larger than those in Préalpes de Digne. This could explain why culling was inefficient to reduce depredations in Vercors when it was efficient in Préalpes de Digne. This statement could nonetheless be contradicted by the massif of Trois-Evêchés, where the highest intensity was 1.32 times larger than in Vercors. However, in the kernel figure of Trois-Evêchés (Figure 3.40), the pre-culling depredation intensity was much more restricted in space towards the culling locations, but also in time, to four periods of a dozen of days. In Vercors, depredation was already spread over space up to 15 km from the culling locations, and was occurring over large period of time before culling. **This could reflect that the culling efficiency could not only depend on the spatial locations, but also on the depredation intensity before the culling application**.

Change the paradigm from individual pastures to local contexts

I believe that the investigation of the reasons of apparition of depredation hotspots makes more sense when encompassing several pastoral surfaces with similar local contexts. Focusing on individualities, by taking the pastures identified as hotspots one by one is an approach currently ongoing by the French administration. If such an approach remains interesting, especially for evaluating the implementation of protective measures, this does not allow an examination of factors that apply at a larger scale. These factors encompass several pastures, and could be related to wolf individuality, wolf territoriality and/or environmental components. To conclude, **a contextual approach could help to generalise an efficient management of depredations to a local context**. For example, management could be adapted to one specific hotspot (as the large hotpot encompassing most of the Alpes-Maritimes) and applied at specific seasons.

For the studies to come

Our approach to study the effects of the observed culling events on depredation required the use of a large number of data, whether it was data on depredations or on culling events. However, if the number of depredations was quite large, especially compared to the studies focusing on North America, the number of culling events was limited. Moreover, data on culling events also lacked variability, with over-representation of certain situations in time (summer–autumn) and in space (hotspots in the south of the French Alpine Arc). Therefore, our approach showed its limits when we investigated the contexts: some contexts only had a dozen of culling events, if not less. This limited the confidence in the results per context. As said in the previous section, the interpretations of these results were also limited because of the non-inclusion of the wolf component in the analysis. Consequently, **more investigations are undoubtedly required to understand the culling effects in France**.

The next investigations could rest upon a similar kernel analysis to ours, but with a larger number of culling events. I do not think it is however

the solution. First, this would postpone the analysis to several years, as the annual culling quota is limited. Second, the lack of variability within culling applications will probably continue in the near future. Third, this would not solve the problem to include the wolf component to the study. Consequently, other approaches should be considered.

One of these approaches could be the experimental study advocated by some international reviews [124, 133, 246]. However, this approach seems difficult to apply in the context of legal protection of wolves, but also because it is hardly feasible to control all possible confounding factors when investigating the effect of culling for predators living on territories of 200 km^2.

Another approach that could be relevant here would be to keep the before/after approach as we made, but focusing on very local contexts and by adding information about wolves (*e.g.* pack or *rendez-vous* site locations). This is an approach that was considered during my thesis. There were four study sites in the French Alpine Arc (Canjuers in Var, Roya in Alpes-Maritimes, Bure in Hautes-Alpes and Maurienne in Savoie) where the *Réseau Loup-Lynx* deployed its members to collect more biological indices than usual, during the thesis. The goal was to conduct genetic analyses to identify the relatedness between wolves and to have a detailed representation of packs at the study site. These sites were chosen because there were frequently culling that was applied there, in response to a high level of depredations. Moreover, they represented four very distinct contexts, whether it is regarding the environment, the pastoral practices or the wolf historical context. For each of these sites, the repercussions of culling on wolves and therefore on depredations could have been investigated. However, the lack of time to analyse the genetic profiles of the collected indices, but also to process these new data, prevented me to conduct this study.

The local zoom of the interactions between wolves, flocks and their protection is already used by IPRA to study the efficiency of livestock guarding dogs to prevent wolf attacks. Investigating the culling effects would require to adapt this approach by taking into account the wolf component outside the pastoral context, over the whole wolf territory but also on adjacent territories. In this regard, the use of a fine wolf monitoring at the study sites, for example through the use of GPS collars, would be of great help. Moreover, it would be necessary to extend the collection of information: for example the detailed use of pastures by flocks, the implementation of their protective measures, the presence of humans to guard flocks, all shots, including the missing ones, and the attempts of depredations, not only the successful ones etc... To be effective, such an approach would require the combined efforts of multiple stakeholders: OFB and hunters for the culling component and the monitoring of wolves, livestock owners and shepherds for the flock and protection components, along with other organisations such as IPRA or CERPAM to bring their specific expertise. I known this type of localised approach is currently considered by CERPAM (O. Bonnet, *pers. com.*) and also by OFB in the context of the European LIFE program WolfAlps (R. Simon, *pers. com.*).

Therefore, a field approach as this one would require a large amount of effort to collect data. The duration of such study would probably be limited in time. Consequently, the number of culling events involved

in such study would probably be limited too. This is where the IBM developed in Chapter 1 and Chapter 2 could play its full role. The field study would help to precise the large unknown portions of the model. For example, by knowing the depredation behaviour of wolves, the hypotheses we tested in Chapter 2 could be transformed into known modelled behaviour. The IBM would therefore help to replicate, *in silico*, the field studies which are limited by resources. The other way, field studies would increase the interest of our IBM. To conclude, **I believe modelling and field studies are complementary: combining both approaches help to fill the gaps of each approach, and therefore to reinforce our understanding**.

The next step to understand the culling effects in France...

... would be to conduct **studies on a reduced scale**, encompassing several pasture surfaces and at most 2–3 adjacent wolf territories, in order to acquire a detailed information about the three interacting components, wolves, flocks and culling. This approach would not allow a regional scope, but would allow less approximation and uncertainty compared to any analysis encompassing a large study area as the one we provided in Chapter 3, where approximations are inevitable. For example, the correction for pastoral use could be exact, instead of using a regional census which lacks of updates and of information regarding the implementation of protective measures.

The multiplication of such approaches would provide, piece after piece, context after context, the emergence of a complete understanding of the culling effects in France. This could also help to precise the hypotheses about the wolf depredation behaviour in the IBM, that would allow the modelling of the culling effects on the long term, at a local scale.

Synthese en francais

Synthèse 6

6.1 Contexte

Le retour du loup gris (*Canis lupus*) en France au début des années 1990 s'est accompagné d'attaques (ou *déprédations*) sur les troupeaux domestiques, notamment dans les massifs à fort intérêt pastoral pour les ovins. Pour prendre en compte cette contrainte environnementale, l'État indemnise les dommages sur les troupeaux domestiques imputés au loup et subventionne la mise en place de mesures de protection des troupeaux. Depuis 2004, cette stratégie est définie dans un Plan national d'actions (PNA), qui a été actualisé à trois reprises.

Classé en Annexe IV de la directive européenne «Habitats-Faune-Flore» que la France a ratifiée, le loup est une espèce strictement protégée et il est interdit de lui nuire, même pour limiter la déprédation. Toutefois, la directive européenne prévoit la possibilité de déroger au statut de protection de l'espèce sous certaines conditions. Ces dérogations sont encadrées en France par un arrêté ministériel qui autorise le prélèvement par le tir d'un nombre de loups défini chaque année, seulement dans les situations jugées les plus difficiles pour les éleveurs.

Dans le même temps, l'État français doit garantir un état de conservation favorable de l'espèce, compte tenu de ses engagements européens. Les actions de gestion telles que les tirs dérogatoires ne doivent pas nuire à la viabilité de la population de loups, tout en réduisant les dommages aux troupeaux. Si la viabilité de la population de loups en France a été mesurée par l'expertise collective de 2017 [112], l'efficacité du contrôle létal de grands prédateurs à réduire les dommages est plus difficile à évaluer et fait actuellement débat parmi les scientifiques [7].

6.2 Problématique

Deux théories existent sur le sujet [133]. La première théorie argumente que le contrôle létal permettrait d'éliminer les loups potentiellement spécialisés dans la déprédation, de réduire localement l'abondance du prédateur et de rendre les loups survivants plus méfiants envers l'humain et ses troupeaux [71]. Les risques de rencontres entre prédateurs et bétail s'en trouveraient abaissés, et par conséquent ceux de déprédation également. L'autre théorie avance que le contrôle létal, en prélevant notamment les loups reproducteurs, pourrait déstabiliser voire dissoudre les meutes et provoquer une réorganisation des territoires. Les loups en dispersion dépourvus de leurs congénères, ou ceux nouvellement arrivés sans connaissance préalable du territoire, pourraient alors se rabattre sur les troupeaux domestiques, plus repérables et plus vulnérables que les proies sauvages [51].

Les liens entre contrôle létal et déprédations peuvent donc être envisagés à travers les effets du contrôle sur la population de loups, les trois

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[112]: Duchamp et al. (2017), *Expertise collective scientifique sur la viabilité et le devenir de la population de loups en France à long terme sous la coordination ONCFS-MNHN de : Guinot-Ghestem M., Haffner P., Marboutin E., Rousset G., Savoure-Soubelet A., Siblet J.P., Trudelle L.*

[7]: Lute et al. (2018), 'Conservation Professionals Agree on Challenges to Coexisting with Large Carnivores but Not on Solutions'

[133]: Treves et al. (2019), 'Predator Control Needs a Standard of Unbiased Randomized Experiments With Cross-Over Design'

[71]: Meuret et al. (2021), 'Missing Shots: Has the Possibility of Shooting Wolves Been Lacking for 20 Years in France's Livestock Protection Measures?'

[51]: Imbert et al. (2016), 'Why Do Wolves Eat Livestock?'

composantes formant alors un cycle (Figure 6.1). C'est donc à travers la modification de la population de loups que le contrôle létal peut avoir un effet sur la déprédation. Les changements induits dans la déprédation peuvent en retour agir sur l'application initiale du contrôle létal. L'ensemble de la problématique peut alors être envisagé sous la forme d'un cycle (Figure 6.1). Cependant, il a été beaucoup plus courant jusqu'ici d'étudier directement l'effet du contrôle létal sur les niveaux d'attaques constatés en réponse, plutôt que ce cycle dans sa globalité.

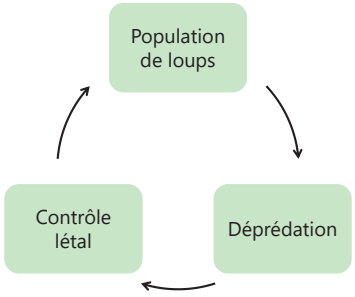

Figure 6.1: Fonctionnement schématique de la gestion des déprédation de loup par le contrôle létal. Crédits : O. Grente

6.3 Revue bibliographique

Peu d'études et des protocoles d'analyse à revoir

Plus d'une quinzaine de revues bibliographiques sur la thématique du contrôle létal appliqué aux grands prédateurs existe dans la littérature scientifique (*e.g.* [133] [83, 134]). Ces travaux s'accordent sur le manque d'études qui analysent l'effet du contrôle létal sur les niveaux de déprédation, quels que soient le type de contrôle et l'espèce visée. Actuellement, à peine une dizaine d'articles scientifiques dans le monde a analysé l'effet du contrôle létal sur les niveaux d'attaques de *Canis lupus*. De plus, toutes ces études ont été réalisées en Amérique du Nord, à l'exception d'une étude en Espagne [67].

[83]: Miller et al. (2016), 'Livestock Losses and Hotspots of Attack from Tigers and Leopards in Kanha Tiger Reserve, Central India'
[134]: Lennox et al. (2018), 'Evaluating the Efficacy of Predator Removal in a Conflict-Prone World'

[67]: Fernández-Gil et al. (2016), 'Conflict Misleads Large Carnivore Management and Conservation'

Ces revues insistent également sur la faiblesse des protocoles d'analyse employés, tous prédateurs confondus. Peu d'études utilisent un protocole expérimental, initialement mis en place avec un choix aléatoire de zones test où serait appliqué le contrôle létal, et des zones sans contrôle létal. Ce type de mise en place expérimentale est en effet peu adapté au statut des espèces protégées, qui ne permet pas de faire varier les différents niveaux de prélèvement.

En grande majorité donc, les études procèdent à une analyse rétrospective des données issues de contrôle létal déjà mis en place dans le cadre d'une gestion, et non pas selon un protocole scientifique établi au préalable [133].

Ces études comparent des zones où le contrôle létal a été appliqué et d'autres où il ne l'a pas été, ou bien comparent les situations avant et après l'application d'un contrôle létal dans une même zone. Cependant, ces études risquent d'attribuer au contrôle létal les fluctuations observées dans les niveaux de déprédation, alors que celles-ci peuvent être dues à d'autres différences entre les exploitations agricoles (environnementales, pastorales...) ou au sein d'un même pâturage au cours du temps [133].

Enfin, d'autres études rétrospectives cherchent plutôt à établir un lien direct entre les niveaux de déprédation et la quantité de prédateurs prélevés, en adoptant une approche corrélative. Celles-ci ne permettent pas de distinguer la cause de l'effet, ce qui peut conduire à des interprétations erronées. Plus faciles d'application en termes d'analyse, elles sont surreprésentées, et celles qui se penchent sur le loup ne font pas exception puisqu'elles en représentent les deux tiers. Le tiers restant est composé d'études rétrospectives non corrélatives, aucune étude sur le loup n'étant expérimentale à ce jour.

Des études aux conclusions contradictoires

La faiblesse des protocoles d'analyse employés conduit à des conclusions divergentes, parfois pour un même jeu de données d'attaques et de prélèvements. C'est le cas pour trois études corrélatives qui analysent 25 ans de données dans les états américains de l'Idaho, du Montana et du Wyoming [100, 140, 141]. L'étude de 2017, qui corrige les biais méthodologiques des études de 2014 et 2016, conclut que durant la phase de recolonisation du loup, le nombre de déprédations augmente malgré l'application du contrôle létal. Pendant cette période, la croissance de la population excède les prélèvements, ce qui a pour effet d'augmenter les effectifs de loups. Cette croissance populationnelle peut alors naturellement expliquer la hausse du nombre d'attaques selon les auteurs. Au contraire, [100] identifiaient le contrôle létal comme la cause directe de l'augmentation du nombre de dommages, car ils omettaient d'intégrer la croissance de la population de loups dans leurs analyses, les conduisant à une erreur d'interprétation. [140] concluent d'ailleurs que lorsque la phase de recolonisation laisse place à celle de stabilisation, au cours de laquelle la population de loups n'augmente plus, alors le contrôle létal a pour effet de diminuer le nombre de déprédations.

[100]: Wielgus et al. (2014), 'Effects of Wolf Mortality on Livestock Depredations'
[140]: Kompaniyets et al. (2017), 'Modeling the Relationship between Wolf Control and Cattle Depredation'
[141]: Poudyal et al. (2016), 'Wolf Lethal Control and Livestock Depredations'

Les études non corrélatives mais rétrospectives ne permettent pas non plus de trancher sur la problématique. [97] démontrent que le piégeage d'un loup mâle adulte après une attaque réduit le risque de réapparition des attaques de loup au sein de la ferme[1] par rapport aux attaques qui ne sont pas suivies d'un piégeage effectif. Cependant, cette réduction reste faible et, à 4 km de la ferme, est également observée lorsque le piège est posé mais qu'aucun loup n'est capturé.

[97]: Harper et al. (2008), 'Effectiveness of Lethal, Directed Wolf-Depredation Control in Minnesota'
1: jusqu'à 4 km autour de la ferme

Avec une approche comparable à [97], [96] notent que le contrôle létal permet d'allonger significativement le délai avant la prochaine attaque à l'échelle du territoire de la meute. Enfin, [52] observent dans le Michigan une tendance à la baisse du risque de réapparition d'une attaque de loup suite au contrôle létal, sur une superficie d'environ 3 km^2 centrée sur l'attaque initiale. En revanche, ils observent une tendance à la hausse de ce risque lorsque l'analyse est faite à une plus grande échelle, sur 90 km^2, traduisant un report potentiel des attaques sur les troupeaux voisins. Cependant, ces deux tendances restent faibles et ne sont pas statistiquement significatives.

[96]: Bradley et al. (2015), 'Effects of Wolf Removal on Livestock Depredation Recurrence and Wolf Recovery in Montana, Idaho, and Wyoming'
[52]: Santiago-Avila et al. (2018), 'Killing Wolves to Prevent Predation on Livestock May Protect One Farm but Harm Neighbors'

Ce que l'on sait en France

La situation en France est différente de celle qui a cours en Amérique du Nord, notamment en ce qui concerne les pratiques pastorales et le dispositif lié au contrôle létal. Jusqu'à présent, il existe surtout un rapport non revu par les pairs qui s'est penché sur le cas français. Il s'agit du rapport de Master 2 de [248]. Cependant, elle n'analyse pas l'effet des tirs à proprement parler, mais celui de l'autorisation des arrêtés préfectoraux autorisant le tir. Sa période d'analyse correspond aux arrêtés de 2009 à 2011, et à la mort dérogatoire de seulement 4 loups.

[248]: Le Cam (2012), *Evaluation de l'efficacité de la mise en place de tirs de défense ou de prélèvement sur les attaques des troupeaux domestiques par le loup Canis lupus*

Elle utilise une approche innovante de comparaison de type avant-après le décret en testant plusieurs échelles spatiales et temporelles et en

appliquant une correction pour la dynamique des attaques liées à la dynamique pastorale (et non à celle des tirs).

Son analyse montre que le nombre d'attaques de loup sur un troupeau baisse significativement jusqu'à la fin de l'année une fois que la dérogation de tir visant à le protéger entre en vigueur, en comparaison avec la période de 30 jours avant l'autorisation du décret. Ces résultats rejoignent ceux de [97] sur l'effet de dissuasion d'une présence humaine renforcée. [248] démontre également que cet effet est toujours significatif lorsque l'on s'éloigne de la ferme, mais qu'il est de moins en moins important au fur et à mesure que la distance à la ferme augmente, jusqu'au massif.

Il faut cependant noter que les échelles temporelles et spatiales pour lesquelles cette baisse est significative varient selon la correction employée pour la dynamique pastorale.

6.4 Méthodes

Finalement, comme sur le plan international, les effets du contrôle létal sur la population de loups restent encore méconnus en France. La thèse a pour objectif d'évaluer ces effets et s'appuie sur les données de mise en œuvre des tirs dérogatoires réalisés en France depuis 2011. Ces données, essentiellement issues du massif alpin, concernent les prélèvements de loups tués par un tir dérogatoire.

Effet des tirs de loup sur les attaques

Suite aux lacunes identifiées sur la problématique grâce à la revue bibliographique, quatre points clés ont été identifiés pour que l'étude adopte la méthodologie la plus robuste possible.

Un protocole avant/après les tirs

L'utilisation de données déjà collectées permet de réaliser une étude, non pas expérimentale, mais rétrospective. Parmi les approches rétrospectives possibles, la comparaison « intra-site » a été préférée (c.-à-d. avant vs après l'application du tir au sein du même site) plutôt que la comparaison « inter-site » (c.-à-d. entre des sites avec tir vs sans tir). En effet, si une situation environnementale ou pastorale peut changer au cours du temps, affaiblissant alors l'analyse, on s'attend cependant à ce que ces variations soient moins élevées que les différences entre plusieurs pâturages.

La nécessaire prise en compte des échelles spatiales et temporelles

Les études citées sur le loup évaluent souvent les effets du contrôle létal seulement lorsque qu'un certain laps de temps s'est écoulé, par exemple un an après le contrôle [140], plutôt que de façon continue tout au long de l'année après le contrôle [52].

De plus, les échelles spatiales analysées sont souvent inappropriées aux rythmes et aux mouvements des animaux dans leurs territoires.

Beaucoup d'études analysent le phénomène à des échelles supérieures à 1000 km^2, ou bien n'analysent pas les risques de report de la déprédation sur les fermes voisines, à l'exception de [52].

L'un des enjeux de l'étude concerne l'identification des « bonnes » échelles spatiales et temporelles auxquelles se produisent les effets des tirs. Afin de ne pas négliger les potentiels reports de déprédation sur les autres pâturages, le principe sera d'analyser les effets des tirs sur les niveaux d'attaques le long d'un gradient spatial et temporel continu autour des tirs.

Distinguer l'effet des tirs de la dynamique saisonnière des attaques

Un autre enjeu majeur de l'étude est de dissocier la dynamique saisonnière des attaques, induite par les pratiques pastorales de transhumance, de celle qui est potentiellement modifiée par les tirs. En effet, le nombre d'attaques a naturellement tendance à diminuer à l'automne car les troupeaux quittent les unités de pâturage d'altitude pour retrouver les zones d'intersaison, puis les exploitations. Cette tendance naturelle à la baisse doit alors être dissociée de celle potentiellement provoquée par les tirs.

Pour cela, trois techniques ont été utilisées. La première a été de restreindre très fortement l'analyse temporelle autour des prélèvements : on compare les niveaux d'attaques 20 jours avant les prélèvements à ceux observés 20 jours après. De cette manière, on peut espérer réduire les risques de variations de l'utilisation des pâtures par les troupeaux.

La deuxième technique a consisté à corriger les résultats obtenus sur une période temporelle plus grande, de 90 jours avant et 90 jours après les prélèvements. Nous avons testé deux corrections. La première correction consistait à simuler l'utilisation pastorale selon les données selon le recensement pastoral de l'IRSTEA en 2012-2014. La deuxième correction consistait à simuler la dynamique des attaques sans l'effet des tirs, à l'image de la correction utilisée par [248].

Approche intégrée de simulations

Jusqu'à présent, nous étudiions directement l'effet des tirs sur les niveaux d'attaques constatés en réponse, sans prendre en compte explicitement les effets sur la population de loups ni les effets rétroactifs des niveaux d'attaques sur l'application du contrôle. Pour pallier cette lacune, nous avons mené un travail de simulation du cycle entier de la Figure 6.1, en modélisant le fonctionnement d'une population de loups, mais aussi plusieurs scénarios concernant le comportement de déprédation chez le loup, et plusieurs scénarios de tirs.

Cette approche est basée sur des modèles informatiques. Elle a pour but de donner un aperçu des effets potentiellement observables dans une population de loups suite aux tirs, par exemple sur la reproduction, la stabilité des couples reproducteurs ou la dispersion. Elle permet d'explorer la validité de chacune des hypothèses 1 et 2 de la Figure 6.1.

Les points chauds de déprédation

En dehors de l'effet des tirs, il nous a paru également important d'inclure une analyse spatiale de l'organisation des attaques dans l'arc alpin, et de son évolution au cours du temps. Nous avons corrigé cette analyse par la distribution spatiale des troupeaux de moutons sur les pâturage, mais également la taille des troupeaux et leur temps de pâturage, qui conditionnent le risque premier de déprédation. L'objectif de cette analyse était double.

Tout d'abord, nous souhaitions explorer l'organisation spatiale des attaques en fonction de la territorialité des loups. Le but était de comprendre si la territorialité pouvait expliquer cette organisation ou non, et si cette dernière changeait au cours de la recolonisation du loup.

Ensuite, il s'agissait d'identifier les points chauds de déprédations à l'échelle des surfaces pastorales, principalement pour aider la gestion des attaques en France. Regrouper les pâturages qui font partie des mêmes points chauds de déprédation permet de coordonner plus efficacement la gestion des attaques, car cela permet d'identifier chaque groupe de pâturages répondant à la même dynamique d'attaques, qui est surement liée à un même jeu de facteurs. De plus, la correction par la présence ovine permet d'identifier les petits troupeaux ou ceux pâturant très peu de temps. Ces troupeaux n'engendrent souvent pas un niveau d'attaques comparable aux pâturages des points chauds traditionnellement identifiés par l'administration, mais leurs niveaux de prédation sont tout de même supérieurs à ce qui serait attendu selon leur faible présence en pâturage.

6.5 Résultats

Approche intégrée

Les résultats principaux de la simulation peuvent être résumés dans le tableau 6.1.

Notre modèle soutient l'hypothèse 1 dans deux contextes de vulnérabilités relatives des proies. Ainsi, quand le bétail est moins ou autant vulnérable que les proies sauvages, les mesures létales sont efficaces pour réduire la déprédation à travers une réduction de la population de loups. La rotation des meutes était plus rencontrée pour ces deux contextes lorsque le contrôle létal était appliqué par rapport à quand il ne l'était pas, mais la déstabilisation des meutes n'empêchait pas le contrôle létal d'être efficace dans la réduction des niveaux de déprédation.

Dans le contexte où le bétail est plus vulnérable que les proies sauvages, les mesures létales ne permettent pas de changer les niveaux de déprédation. Ce contexte est spécifique à l'hypothèse 2 où les individus avec de plus faibles capacités de chasse (jeunes loups ou loups solitaires) sont les plus enclins à déprédater. La proportion de loups tués étaient en fait trop faible pour monter un effet. Ceci était dû aux choix de modélisation, notamment à celui d'attribuer un indice de déprédation négatif aux loups les moins enclins à déprédater dans ce scénario, au lieu d'augmenter l'indice de déprédation de ceux plus enclins à déprédater.

Par conséquent, **nous ne pouvons conclure avec certitude sur les effets du contrôle létal modélisé sous le contexte 1 où les loups avec de plus faibles capacités de chasse (jeunes loups ou loups solitaires) sont les plus enclins à déprédater**.

Table 6.1: Les résultats résumés du modèle individu-centré complet, liés à l'hypothèse des capacités de chasse, résumés pour les deux niveaux individuel ("niv. ind.") et individuel et meute ("niv. ind. et meute"). Les "mécanismes responsables" sont les mécanismes liés à la dynamique de la population qui étaient responsables de l'effet du contrôle létal sur la déprédation. Les "effets secondaires" sont les mécanismes affectés par les contrôles létaux mais qui sont sans conséquence sur la déprédation. Les "hypothèses vérifiées" correspondent aux deux hypothèses contradictoires sur l'effet du contrôle létal.

	Contexte 0	Contexte 1	Contexte 2
Vulnérabilité du bétail	= Vulnérabilité proies sauvages	> Vulnérabilité proies sauvages	< Vulnérabilité proies sauvages
Risque de déprédation plus élevé	Adultes en meute (besoins énergétiques)	Subadultes (niv. ind.) ou subadultes, loups seuls et disperseurs (niv. ind. et meute)	Adultes (niv. ind.) ou adultes et en meute (niv. ind. et meute)
Effet du contrôle létal	Réduit la déprédation	Pas de changement	Réduit la déprédation
Mécanismes responsables	Réduction de la population	Aucun	Réduction de la population
Effets secondaires	Rotation des meutes accentuée et plus faible taux de disperseurs	Un taux de disperseurs légèrement plus faible	Rotation des meutes accentuée et plus faible taux de disperseurs
Hypothèse vérifiée	Hypothèse 1	Aucune	Hypothèse 1

Effet des tirs de loup sur les attaques

L'analyse des effets du contrôle létal avec les données observées en France doit être divisée en deux catégories.

1. L'analyse des effets de la mort d'un seul loup sur les niveaux de déprédation sans aucun distinction,
2. L'analyse explorant la variabilité de ces effets selon la localisation, la date, les classes de tir (défence ou prélèvement) et le sexe du loup mort.

L'analyse générale indique que les déprédations sont agrégées à une courte distance des évènements de tirs quand l'analyse est conduite sur 10 km. Les déprédations sont trouvées en grande quantité avant et après les évènements de tirs. Quand tous les évènements de tirs sont regroupés et corrigés par l'utilisation pastorale, les tirs ne semble pas pouvoir arrêter les déprédations après leur application, mais semblent pouvoir réduire la durée sur laquelle ces déprédations apparaissent.

Cependant, le regroupement de tous les évènements de tirs peut masquer des résultats très variables entre ces évènements, qui résultent de différentes situations, notamment selon la localisation des tirs. Ces résultats sont résumés dans le tableau 6.2. La grande variabilité dans ces résultats nous montre que nous devons être extrêmement prudents quand nous

analysons tous les évènements de tirs ensemble sans considérer leurs caractéristiques.

J'en conclus que les effets des tirs de loup en France sont hautement variables selon les contextes, et impliquent différents résultats. La majorité de ces effets n'impliquent pas de changement ou une réduction de la déprédation, et une minorité indique une augmentation de la déprédation. Les reports spatiaux de déprédations peuvent être suspectés dans 7 contextes sur 25, et les élalements spatiaux de déprédations dans 3 contextes sur 25.

Cependant, il faut être précautionneux avec les résultats du tableau 6.2. Ils sont très synthétisés and si un contexte en particulier vous intéresse, je vous recommande fortement de regarder la figure correspondante dans le chapitre Chapter 3 (Effects of culling on depredation) on page 127 et de la comparer aux figures des autres groupes de tirs pour la même variable (par example la variable "Massif").

Les points chauds de déprédation

L'analyse de l'organisation spatiale des attaques dans l'arc alpin a révélé que l'agrégation des attaques en points chauds n'était probablement pas expliquée uniquement par le facteur de territorialité d'une seule meute, et que d'autres facteurs doivent contribuer à la formation des points chauds. En effet, la taille moyenne d'un point chaud inclut plusieurs territoires de meutes. Par conséquent, des conditions environnementales propices à la déprédation doivent aussi expliquer l'agrégation des déprédations à ces zones localisées, comme le Mercantour ou Canjuers.

Au fur et à mesure que le temps passe, l'agrégation des attaques semble s'atténuer dans l'arc alpin. Les déprédations ont tendance à s'uniformiser à travers l'arc alpin, les points chauds concernent alors des surfaces de plus en plus grandes.

Cette homogénéisation de la déprédation à travers la région peut être due à un risque d'homogénéisation du risque de déprédation, potentiellement à cause d'un nombre croissant de troupeaux protégés avec le même lot de mesures. Dans la carte des cercles de prédation utilisés par la France pour allouer les subventions des mesures de protection non létales en 2020, presque toutes les communes dans l'arc alpin correspondent aux cercles 0 et 1, qui accordent les mêmes subventions pour les mêmes mesures de protection non létales.

Cette tendance générale à l'homogénéisation ne doit pas non plus masquer la présence de petits points chauds, parfois réduit à une seule surface pastorale. Contrairement aux grands points chauds, ceux-là réfèrent à un phénomène plus ponctuel, car ils peuvent apparaître seulement pour une année, sans récurrence. **Je fais l'hypothèse que ces points chauds peuvent refléter des conditions brèves propices à la déprédation, liées à la météo, à des afaiblissements dans la protection ou à des loups spécifiques par exemple, alors que les grands points chauds peuvent plutôt refléter des conditions environnementales durables qui favorisent la déprédation**.

Pour l'étude de manière générale, que cela soit pour l'organisation spatiale des attaques ou l'identification de points chauds, la correction

Table 6.2: Résumé des résultats de l'analyse par calculs de noyaux de l'effet des tirs sur les niveaux de déprédation avec les données observées en France, quand on explore la variabilité de l'effet des tirs selon leurs caractéristiques. Le total indique le nombre d'évènement de tirs analysés associé à chaque groupe de caractéristiques. L'effet du tir sur les niveaux de déprédation est codé avec ↘ pour la réduction des déprédations, ∅ (pour aucun changement), ↗ (pour une augmentation des déprédations) et '?' pour un signal peu clair. **L'intensité de l'effet n'est pas reporté dans le tableau**. Le report de déprédation se rapporte à la possibilité que les déprédations soient toujours présentes après les tirs, mais à d'autres endroits comparés à ceux d'avant-tir. L'étalement de déprédation se rapporte à la possibilité que les déprédations soient toujours présentes après les tirs aux mêmes endroits qu'avant ceux-ci, mais en plus à d'autres endroits. Si des reports ou des étalements de déprédations sont suspectés, ils sont codés par ✓, s'ils ne le sont pas, ils sont codés par ✗ ou si ce n'est pas clair, cela est codé par '?'. Tous les évènements de tirs correspondent à la mort d'un loup seulement, qui est indépendant des autres prélèvements, exceptés pour les 24 groupes de prélèvements en interaction et simultanés ('Interaction, sim.') et les 26 groupes de prélèvements en interaction mais non-simultanés ('Interaction, non-sim.') dans 'Combinaison de tir'. **Le tableau n'est qu'un guide de lecture aux figures du Chapter 3, et non une substitution**.

Variable		Total	Effet	Report	Etalement
Massif	Mercantour-Argentera	44	∅	✓	✗
	Préalpes d'Azur	33	?	✗	✗
	Trois Evêchés	18	↘	✓	✗
	Vanoise	18	∅	✗	✗
	Vercors	18	↗	✗	✓
	Préalpes de Digne	12	↘	✓	✗
	Ecrins	12	?	✓	✓
	Canjuers	11	?	✗	✗
	Cerces	10	↘	✓	✗
Altitude	Montagnard	136	↘	✗	✗
	Subalpin	75	∅	✗	✗
	Collinéen	19	∅	✗	?
Saison du loup	Automne (sept.–oct.)	75	↘	✗	✗
	Site de RDV (juil.–aout)	72	∅	✗	✓
	Tanière (avr.–juin)	43	↗	✗	✗
	Hiver (nov.–jan.)	34	↗	?	✗
	Accouplement (fév.–mars)	12	↘	✗	✗
Sexe tiré	Femelle	91	?	✓	✗
	Mâle	103	∅	✗	✗
Combinaison de tir	Unique	236	∅	✗	✗
	Interaction, sim.	24	↘	✓	✗
	Interaction, non-sim.	26	↘	✗	✗
Classe de tir	Défense renforcée	95	∅	✗	✗
	Défense simple	78	↘	✗	✗
	Prélèvement	63	↘	✗	✗

par la taille des troupeaux ou la durée de pâturage était essentielle. Les résultats étaient différents lorsque nous ne considérions pas ces variables qui structurent en premier la répartition des attaques au sein des surfaces pastorales. En particulier, les points chauds qui incluent peu de surfaces pastorales, avec de petits troupeaux ou pâturant peu de temps, sont plus probables d'être détectés lorsque l'on inclut la correction de l'occupation pastorale dans nos analyses.

6.6 Les perspectives

La nécessaire prise en compte des contextes

Si, par chance, des gestionnaires en charge des déprédations de loup ont lu ma thèse, ils pourraient être très confus au sujet de l'utilisation du contrôle létal. Est-il efficace ou non à réduire les déprédations ? Je sais qu'une réponse binaire aurait grandement facilité le choix d'appliquer ou non le contrôle létal. Cependant, parce que le processus de déprédation est complexe, j'ai bien peur que les effets du contrôle létal le soient aussi. Comme [131] l'a écrit au sujet des prélèvements de grands prédateurs, *'aucune prescription unique n'est appropriée à toutes les situations conflictuelles'*. En France, il y a une multitude de situations conflictuelles concernant les déprédations de loup.

[131]: Treves et al. (2005), 'Evaluating Lethal Control in the Management of Human–Wildlife Conflict'

Je vais néanmoins tenter de connecter d'extraire de potentielles applications depuis nos résultats. Notre étude sur les points chauds de déprédations a montré que celles-ci avaient tendance à former de grands et récurrents foyers qui concernaient chacun un groupe de pâturages plutôt que des pâturages isolés. Il pourrait y avoir une dynamique spécifique homogène des déprédations à l'intérieur de chacun de ces foyers. Ces foyers pourraient délimiter des zones de gestion, où le contrôle létal ou d'autres mesures pourraient être spécifiquement adaptés à ces contextes.

Une évaluation de la situation de chaque foyer pourrait être réalisée. Cette évaluation ne devrait pas seulement être restreinte à décrire les pratiques pastorales, mais devrait aussi être orientée à combler les manques dans notre connaissance du comportement de déprédation. Ce besoin est très bien résumé par [237], p.5 :

[237]: Borelli et al. (2021), *Le loup dans le système pastoral. Rapport CanOvis IPRA-FJML 2013-2018.*

> *Un des facteurs majeurs qui peut moduler l'efficacité de la protection est le prédateur lui-même. Paradoxalement, il s'agit de la variable la moins étudiée.*

Quand [237] mentionnent la protection, ils se réfèrent principalement aux chiens de protection. Cependant, je pense que cette affirmation pourrait être appliquée aussi aux prélèvements. Nous ne savons toujours pas s'il y a des types de loup spécifiques qui tentent et/ou réussissent les déprédations, notamment en regard du contexte. A la fin du Chapitre 2 sur l'IBM, j'ai mentionné le contexte du milieu pastoral ouvert de haute altitude, et les pâturages embroussaillés de plus basse altitude. Il pourrait y avoir beaucoup plus de contextes que ces deux contextes très généraux.

Une protection, ou une action comme le prélèvement, qui est efficace dans l'un de ces contextes, pourrait être inefficace dans un autre, parce que le comportement de prédation n'est pas le même. C'est la raison pour laquelle nous nous sentons impuissants concernant les effets du contrôle létal. Même quand cette thèse fournit des indices concernant la relation entre le prélèvement et la déprédation pour les différents contextes du Chapitre 3, quelque chose manque toujours pour pleinement interpréter et comprendre ces résultats : il s'agit de la composante "loup". En ce sens, l'IBM, même s'il était un exercice académique et non un outil de gestion, a montré que les changements dans les comportements de déprédation pouvaient modifier les effets des prélèvements.

Du point de vue des résultats des prélèvements observés en France, il y a cependant plusieurs conseils qui peuvent être prodigués concernant l'application des prélèvements. Premièrement, **il pourrait y avoir des saisons qui pourraient être plus appropriées que d'autres pour s'assurer que le prélèvement a les effets escomptés sur les déprédations**. Les prélèvements durant les périodes les plus cohésives pour le loup (hiver et tanière) sont associés à une augmentation de la déprédation. Le contrôle létal durant ces saisons pourrait peut-être favoriser les dislocations des meutes ou la reproduction multiple. D'un autre côté, le prélèvement durant les périodes de fortes tensions (automne et reproduction) ont conduit à une réduction des déprédations sans report ou étalement des déprédations sur les pâturages adjacents. C'est cohérent avec les travaux de [254] qui ont montré qu'il y avait une saison d'application des prélèvements de coyotes plus efficace que d'autres[2].

[254]: Blejwas et al. (2002), 'The Effectiveness of Selective Removal of Breeding Coyotes in Reducing Sheep Predation'

2: Cependant dans leur étude, c'était la période de nourrissage des jeunes (Mai–Août) qui a présenté une réduction des déprédations, alors que cette période de Mai à Août correspond à la tanière et au site de rendez-vous chez le loup.

Deuxièmement, des contextes locaux pourraient être plus appropriés que d'autres pour s'assurer que les prélèvements ont bien l'effet escompté sur les déprédations. Nous avons vu que les prélèvements dans les Préalpes de Digne ou le massif des Trois-Evêchés étaient associés à une réduction de la déprédation, alors que les prélèvements semblaient induire un étalement voire même une augmentation des déprédations dans le Vercors. Cependant, quand nous comparons les contextes, nous ne devrions pas oublier de comparer aussi leurs intensités de déprédation, et pas seulement l'effet général des prélèvements. Par exemple, la plus forte intensité dans le Vercors était 2,61 plus grande que celle dans les Préalpes de Digne. Cela pourrait expliquer pourquoi les prélèvements étaient inefficaces pour réduire les déprédations dans le Vercors, alors qu'ils l'étaient dans les Préalpes de Digne. Cette affirmation pourrait être néanmoins contredite par le massif des Trois-Evêchés, où la plus forte intensité était 1,32 fois plus grande que dans le Vercors. Cependant, dans la figure des Trois-Evêchés (Figure 3.40), la forte intensité de déprédation avant les prélèvements était beaucoup plus restreinte dans l'espace, vers la localisation des prélèvements, mais aussi plus restreinte dans le temps, à quatre périodes d'une dizaine de jours. Dans le Vercors, la déprédation était déjà étendue dans l'espace dans les 15 kilomètres autour des prélèvements, et se produisait sur de plus grands laps de temps qu'avant le prélèvement. **Par conséquent, l'efficacité du contrôle létal pourrait non seulement dépendre de l'endroit où il est appliqué, mais aussi de l'intensité de la déprédation avant son application**.

Des pâturages individuels aux contextes locaux

Etudier les causes des foyers de prédation peut se faire à l'échelle des pâturages individuels ou à l'échelle de plusieurs surfaces pastorales qui sont soumises à des contextes locaux similaires. Se focaliser sur les individualités, en prenant un à un les pâturages identifiés comme des foyers, est une approche actuellement utilisée par l'administration française. Si une telle approche reste intéressante, en particulier pour évaluer la mise en place des mesures de protection, cela ne permet pas une examination des facteurs qui s'appliquent à plus large échelle. Ces facteurs englobent plusieurs pâturages et pourraient être en relation avec des loups particuliers, des territoires des loups et/ou liés à l'environnement. Pour conclure, **une approche contextuelle pourrait aider à adopter une gestion efficace des déprédations adaptée à chaque contexte local**. Par exemple, la gestion par les tirs létaux pourrait être adaptée à un point chaud spécifique et appliquée à des saisons spécifiques.

Pour les études à venir

Notre approche pour étudier les effets des prélèvements observés sur la déprédation a requis l'utilisation d'un grand nombre de données. Si le nombre de déprédations était relativement grand, en particulier comparé aux études se focalisant sur l'Amérique du Nord, le nombre de prélèvements était plus limité. De plus, les données sur les prélèvements manquaient de variabilité, avec une sur-représentation de certaines situations dans le temps (été–automne) et dans l'espace (foyers dans le sud de l'arc alpin français). Par conséquent, notre approche a montré ses limites quand nous nous sommes penchés sur les contextes : certains contextes avaient une douzaine de prélèvements seulement, si ce n'est moins. Cela a limité la fiabilité des résultats donnés par contexte. Comme mentionné dans la section précédente, les interprétations de ces résultats étaient aussi limitées à cause de l'absence de la composante "loup" dans l'analyse. Par conséquent, **plus d'investigations sont indubitablement requises pour connaître les effets des tirs en France**.

Les prochaines investigations pourraient reposer sur des analyses de calculs par noyaux similaires aux nôtres, mais avec un plus grand nombre de prélèvements. Cependant, je ne pense pas que cela soit la solution. Premièrement, cela repousserait l'analyse à plusieurs années, puisque les prélèvements sont limités par un seuil. Deuxièmement, le manque de variabilité de l'application des tirs va probablement continuer à l'avenir. Troisièmement, cela ne résoudra pas le problème d'inclure la composante "loup" dans l'étude. Par conséquent, d'autres approches devront être considérées.

L'une de ses approches pourrait être l'étude expériementale préconisée par certaines revues bibliographiques internationales [124, 133, 246]. Cependant, cette approche semble difficile à appliquer dans un contexte de protection légale des loups, mais aussi parce qu'il est difficile de contrôler tous les facteurs confondants possibles en étudiant l'effet du contrôle létal pour des prédateurs vivant sur des territoires de 200 km^2.

Une autre approche qui pourrait être pertinente ici serait de conserver l'approche avant/après comme la nôtre, mais en se focalisant sur des contextes locaux et en ajoutant de l'information au sujet des loups (*e.g.* meute ou localisations des sites de rendez-vous). Cette approche a été considérée pendant la thèse. Quatre sites d'étude dans l'arc alpin français (Canjuers dans le Var, Roya dans les Alpes-Maritimes, Bure dans les Hautes-Alpes et Maurienne en Savoie) ont été prospectés à haute fréquence par les correspondants du Réseau Loup-Lynx au cours de la thèse, afin de récolter un maximum d'indices biologiques. Le but était de conduire des analyses génétiques de ces indices pour identifier l'apparentement entre les loups et avoir une représentation détaillée des meutes aux sites d'étude. Ces sites ont été choisis parce que le contrôle létal y était fréquemment appliqué, en réponse à un niveau de déprédations élevé. De plus, ils représentaient quatre contextes très distincts, que cela soit en rapport avec l'environnement, les pratiques pastorales ou le contexte historique de présence du loup. Pour chacun de ces sites, les répercussions des prélèvements sur les loups survivants et par conséquent sur les déprédations auraient pu être étudiées. Cependant, le manque de temps pour faire analyser les profils génétiques des indices collectés, mais surtout pour traiter ces données génétiques, m'a empêchée de mener à bien cette approche.

Etudier localement les interactions entre les loups, les troupeaux domestiques et leurs protections est une approche déjà utilisée par l'IPRA pour étudier l'efficacité des chiens de protection à empêcher les déprédations de loups. Etudier les effets du prélèvement pourrait nécessiter d'adapter cette approche en prenant en compte la composante "loup" en dehors du contexte du troupeau protégé, c'est-à-dire sur l'ensemble du territoire de la meute mais aussi sur les territoires adjacents. A cet égard, l'utilisation d'un suivi fin des loups, par exemple à travers l'utilisation de colliers GPS, serait d'une grande aide. De plus, il serait nécessaire d'étendre la collecte d'informations, avec par exemple l'utilisation détaillée des pâturages par les troupeaux, la mise en place des mesures de protection, la présence humaine pour garder les troupeaux, tous les tirs, y compris les manqués, ainsi que les tentatives de déprédations, pas seulement les réussies, etc... Pour être possible, une telle approche nécessiterait des efforts combinés de plusieurs acteurs : OFB et chasseurs pour la composante "contrôle létal" et le suivi des loups, les éleveurs et bergers pour la composante "troupeau", avec des organismes comme l'IPRA ou le CERPAM pour apporter leurs expertises spécifiques. Je sais que ce type d'approche localisée est actuellement considérée par le CERPAM (O. Bonnet, *com. pers.*) mais aussi par l'OFB dans le contexte du programme européen LIFE WolfAlps (R. Simon, *com. pers.*).

La durée de telles études localisées sera sûrement possible sur un laps de temps relativement limité. Par conséquent, le nombre de prélèvements impliqués dans ce type d'étude sera probablement faible. C'est là où l'IBM développé dans les Chapitres 1 et 2 pourrait jouer un rôle à part entière. L'étude de terrain pourrait aider à préciser les actuelles inconnues du modèle. Par exemple, en connaissant le comportement de déprédation des loups, les hypothèses testées dans le Chapitre 2 pourraient être modélisées en un comportement connu. L'IBM pourrait alors aider à répliquer, *in silico*, les études de terrain qui sont limitées en ressources. Dans l'autre sens, les études de terrain augmenteraient l'intérêt de notre

IBM. Ainsi, **je pense que la modélisation et les études de terrain sont complémentaires : combiner les deux approches aide à combler les lacunes de l'une et de l'autre, et par conséquent à renforcer notre compréhension**.

La prochaine étape pour comprendre les effets des prélèvements en France...

... serait de conduire des études à **une échelle réduite** qui englobe plusieurs surfaces pastorales et au plus 2 à 3 territoires de loups adjacents. Réduire l'échelle d'étude permet d'acquérir une information plus détaillée pour les trois composantes en interaction, à savoir les loups, les troupeaux domestiques et le contrôle létal. Cette approche ne pourrait donc pas avoir une portée régionale. Cependant elle permettrait moins d'approximations et d'incertitudes comparée à une analyse qui englobe une grande aire d'étude (comme l'arc alpin) où les approximations sont inévitables. Par exemple, la correction par l'usage pastoral pourrait être exacte, et éviterait d'utiliser un recensement régional qui manque de mises à jour et d'informations concernant la mise en place des mesures de protection.

La multiplication de telles approches localisées fournirait, pièce après pièce, contexte après contexte, une émergence d'une compréhension complète des effets du contrôle létal en France. Cela pourrait aussi aider à préciser les hypothèses au sujet du comportement de déprédation du loup dans l'IBM. Ce dernier permettrait alors la modélisation des effets des tirs sur le long terme, pour chaque contexte local.

Appendix

The wolf population dynamics | A

This appendix completes Chapter 1 (The wolf population dynamic) on page 32, and contains the full article of:

> Sarah Bauduin, Oksana Grente, Nina Luisa Santostasi, Paolo Ciucci, Christophe Duchamp, Olivier Gimenez, (2020). An individual-based model to explore the impacts of lesser-known social dynamics on wolf populations. *Ecological Modelling*,Volume 433, p.109209. https://doi.org/10.1016/j.ecolmodel.2020.109209

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An individual-based model to explore the impacts of lesser-known social dynamics on wolf populations

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ABSTRACT

The occurrence of wolf populations in human-dominated landscapes is challenging worldwide because of conflicts with human activities. Modeling is an important tool to project wolf dynamics and expansion, and help in decision making concerning management and conservation. However, some individual behaviors and pack dynamics of the wolf life cycle are still unclear to ecologists. Here we present an individual-based model (IBM) to project wolf populations while exploring the lesser-known processes of the wolf life cycle. IBMs are bottom-up models that simulate the fate of individuals interacting with each other, with population-level properties emerging from the individual-level simulations. IBMs are particularly adapted to represent social species such as the wolf that exhibits complex individual interactions. Our IBM projects wolf demography including fine-scale individual behavior and pack dynamics based on up-to-date scientific literature. We explore four processes of the wolf life cycle whose consequences on population dynamics are still poorly understood: the pack dissolution following the loss of a breeder, the adoption of young dispersers by packs, the establishment of new packs through budding, and the different breeder replacement strategies. While running different versions of the IBM to explore these processes, we also illustrate the modularity and flexibility of our model, an asset to model wolf populations experiencing different ecological and demographic conditions. The different parameterization of pack dissolution, territory establishment by budding, and breeder replacement processes influence the projections of wolf populations. As such, these processes require further field investigation to be better understood. The adoption process has a lesser impact on model projections. Being coded in R to facilitate its understanding, we expect that our model will be used and further adapted by ecologists for their own specific applications.

1. Introduction

The gray wolf (*Canis lupus*) has been extirpated from most of the globe during the last century due to its competition with humans for wild prey, depredations on livestock and general persecution (Ripple et al., 2014). Most of the remaining populations were considered endangered in the early 20th century (Mech and Boitani, 2003). However, numerous wolf populations are now under protection regimes and management actions favor species persistence or comeback (Chapron et al., 2014). Even though the presence of this large carnivore may play an important role in maintaining a healthy ecosystem and increase biodiversity, its recolonization is challenging. For example, the impact wolves exert on human activities such as livestock farming (Kaczensky, 1999; Lute et al., 2018), or the increasing threat of hybridization with dogs in human-dominated landscapes (Pilot et al., 2018; Randi, 2011; Randi et al., 2014) require informed and effective management of the populations (Hindrikson et al., 2017). Management interventions may involve control of wolf populations through legal killings (Bradley et al., 2015; Harper et al., 2008; Santiago-Avila et al., 2018) or non-lethal management options (McManus et al., 2015; Treves et al., 2016) such as sterilization of breeders (Donfrancesco et al., 2019; Haight and Mech, 1997). In order to inform

Abbreviations: IBMs, individual-based models; ID, identity; Fig., Figure; ODD, Overview, Design concepts, and Details; popDensStd, wolf density per 1000 km^2 standardized with mean and standard deviation from Cubaynes et al. (2014); sd, standard deviation

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and help managers in making the best decisions, models are needed to forecast the impact of alternative management regimes on the population dynamics and viability of the species (Bull, 2006; Marescot et al., 2013). Not only can models help select the best management strategy among several, but they can also define the most effective application of any particular strategy (e.g., its intensity or frequency) (Haight and Mech, 1997). However, before projecting the impact of external factors on wolf populations, a good understanding of the species life cycle, as well as a reliable model simulating it, is required.

Different types of models have been used to project the dynamics of highly social species such as the gray wolf. Stage-structured models including age-, breeding- or dispersing-specific individual categories have been developed to project population growth rate, and hence are relevant to make projections at the population level (Haight and Mech, 1997; Marescot et al., 2012). Individual-based models (IBMs) have also been used to model population dynamics and have proven to be more flexible to represent species with complex social structure like wolves or coyotes (Chapron et al., 2016; Marucco and McIntire, 2010; Pitt et al., 2003). IBMs are bottom-up models that simulate the fate of individuals interacting with each other and/or their environment. IBMs can include many individual-level mechanisms (i.e., behavioral rules) and therefore can represent complex individual interactions as exhibited by these social species (Chapron et al., 2016; Haight et al., 2002; Marucco and McIntire, 2010; Pitt et al., 2003). Population-level results emerge from the individual-level simulations (Railsback and Grimm, 2012). IBMs are modular models, in that they are built as series of sub-models. Sub-models represent either processes of the species life cycle (e.g., reproduction, mortality) or external factors that modify the population structure (e.g., immigration, management). In this respect, IBMs can be very flexible as sub-models can be independently parameterized, reorganized or removed, or new ones can be added. This flexibility allows researchers to mimic the species life cycle very closely, to test different versions of the model by modifying only some sub-models, as well as testing the impact of external processes, such as different management actions, on simulated populations (Bull et al., 2009; Hradsky et al., 2019).

Researchers have used IBMs to simulate the impact of wolf-removal strategies on depredation and population viability (Haight et al., 2002), to test the robustness of abundance indices (Chapron et al., 2016) or to project the recolonization of the species and the associated risk of depredation (Marucco and McIntire, 2010). The models were all based on the fundamental processes of mortality, reproduction and dispersal. They also enabled individuals to access to the breeder status by various means, such as pack creation or the replacement of a missing breeder in a pack. Additionally, Haight et al. (2002) and Chapron et al. (2016) included supplementary mortality processes mimicking different wolf removal strategies. However, other individual behaviors and social dynamics, not included in these IBMs, are known to occur in the wild. For example, Brainerd et al. (2008) found that the loss of breeders in a pack might disrupt its stability, depending on the pack size and number of remaining breeders, and may induce a pack dissolution. Specifically, small packs with only one breeder left had a high probability of breaking apart and even higher when no breeder remained (Brainerd et al. 2008). In addition, several studies observed that when breeders died in packs, vacant male breeding positions were primarily filled by unrelated individuals, whereas vacant female breeding positions were mostly filled by subordinate females of the same packs, which were most likely the daughters of the former breeding females (Caniglia et al., 2014; Jedrzejewski et al., 2005; Vonholdt et al., 2008). These processes surely play a role in inbreeding avoidance. Another social process affecting wolf population dynamics is the adoption of unrelated individuals within packs. Young lone wolves not holding a territory sometimes join and are adopted, as subordinates, by packs (Mech and Boitani, 2003). Most adoptees are males of 1 to 3 years old (Meier et al., 1995; Messier, 1985). Adoptees seem to represent a non-negligible part of the populations, roughly estimated between 10% and 20% (Mech and Boitani, 2003). However, adoptees are generally not identified in wolf populations as it necessitates genetic sampling and relatedness analyses. The reasons behind this behaviour are still poorly known (Mech and Boitani, 2003). Finally, less common strategies of formation of new reproductive pairs through “budding” or “splitting” may influence the wolf establishment and reproduction dynamics. Budding is when a dispersing wolf pairs with a mature subordinate from an existing pack and they establish a new pack of their own (Brainerd et al., 2008; Mech and Boitani, 2003). Pack splitting has been reported for large packs, mainly in North American wolf populations (Hayes and Harestad, 2000; Jedrzejewski et al., 2004; Meier et al., 1995; Vonholdt et al., 2008). A sub-group of individuals permanently splits off from their original pack to form a new one nearby, often due to the presence of two breeding pairs in the pack (Jedrzejewski et al., 2004; Mech and Boitani, 2003). It differs from budding in that no dispersing individual is involved in the process. Studies on wolf genetics, inbreeding (Caniglia et al., 2014; Vonholdt et al., 2008), hybridization (Fredrickson and Hedrick, 2006) or assessment of management alternatives (Haight et al., 2002; Haight and Mech, 1997) that fail to account for important processes of wolf social dynamics may provide limited or erroneous conclusions, leading to potential inappropriate management decisions. Unfortunately, the processes mentioned above are not often reported from field studies, they are rarely quantified and their details are poorly documented.

Here we present an IBM that we developed to simulate the wolf life cycle while exploring four lesser-known processes of its social dynamics, specifically: the pack dissolution following the loss of a breeder, the adoption by existing packs of young dispersers, the establishment of new packs through budding, and the different types of breeder replacement. Our model explicitly includes interactions between individual wolves, accounting for changes in wolf status (i.e., breeder vs subordinate, resident vs disperser), dispersal, and establishment processes while taking into account density-dependence and individuals' relatedness. While we use literature to parametrize well-known individual behaviors and pack dynamics, we model multiple scenarios based on different parameters, similar to a sensitivity analysis, to explore the lesser-known processes. The variability among model projections reveals processes that most affected wolf population dynamics, therefore indicating life-cycle traits that require further investigation to enhance reliability of population projections. We develop our model using the R language to facilitate its clarity, accessibility and uptake by ecologists. Given the flexibility and modularity of the model structure, our IBM can be easily parameterized according to different values, updated with improved knowledge on wolf dynamics, or modified to be adapted to other specific research or management questions on wolves.

2. Methods

2.1. Wolf IBM

2.1.1. Background information

We calibrate the model for central European wolf populations (i.e., Alps, Apennines). These populations are recolonizing the territory, locally generating conflicts with human activities (Chapron et al., 2014). They have also been well monitored and we have good estimates for their demographic parameters (Marucco et al. 2009, Caniglia et al. 2014). A pack is usually composed of one breeding pair, potentially augmented by several non-breeding subordinates. Mortality causes (e.g., starvation, disease, vehicle collisions, culling, poaching, intraspecific strife) differ among individuals, inducing different mortality rates usually depending on their age (Marucco and McIntire, 2010) or their residence status (Blanco and Cortés, 2007). Moreover, higher population densities cause competition for food, space and mates, and may also induce a higher adult mortality due to intraspecific aggressions (Cubaynes et al., 2014). Following the death of one or both breeders, a pack can persist and breeders can be replaced.

Wolves routinely disperse in response to competition and aggression related to food availability and breeding opportunity within their pack (Mech and Boitani, 2003). Non-breeding wolves are forced to leave the pack because of social drivers regulating group size within the territory (Ballard et al., 1987; Fritts and Mech, 1981; Fuller, 1989; Gese and Mech, 1991; Mech, 1987). In areas of high prey availability, dispersal is postponed (Ballard et al., 1987; Blanco and Cortés, 2007; Jimenez et al., 2017) and is rather triggered by the onset of sexual maturity of young wolves (Gese and Mech, 1991; Messier, 1985; Packard and Mech, 1980) so that most wolves have dispersed from their natal pack by the age of 3 (Gese and Mech, 1991; Jimenez et al., 2017). Given wolves dispersal abilities, individuals may move from one population to another through long distance dispersal (Blanco and Cortés, 2007; Ciucci et al., 2009) in immigration and emigration processes. One of the main processes for dispersing wolves to reproduce is to form a new pack with a dispersing mate of the opposite sex (Mech and Boitani, 2003). Dispersing individuals can also establish a new territory by themselves, waiting for a mate to later join them (Wabakken et al., 2001).

2.1.2. Main model structure

The model simulates the life cycle of the gray wolf using an individual-based structure, including fine-scale individual processes and pack dynamics through a non-spatially explicit approach. The complete description of the IBM following the Overview, Design concepts, and Details protocol ("ODD" protocol) (Grimm et al., 2010, 2006) is provided in Appendix A. Simulated individuals represent wolves that are organized in packs. Each wolf holds a unique ID, a sex (male or female), an age, if it is a resident (i.e., member of a pack) or a disperser, if it attained breeder status or not, and a pack ID to which it belongs (if resident). The model also tracks each wolf's genealogy and each individual has a mother ID and father ID, and a cohort ID (i.e., the year it was born). Wolves are individually aged as pups (1 year old), yearlings (2 years old), or adults ($\geq$ 3 years old). We assume all wolves reach sexual maturity at 2 years old. We consider a pack when one or several individuals establish and become residents. In our model, "dispersers" or "dispersing individuals" include all non-resident individuals, comprising those that are actually dispersing (i.e., that left their natal pack and are dispersing through the landscape searching for an opportunity to establish a new territory and mate), as well as floaters (i.e., nomadic individuals without a territory and available either to replace missing breeders within packs, or to establish a new pack (Mancinelli et al., 2018)). We also consider in our model that a solitary resident wolf holding a territory alone constitutes a pack. Although our IBM is not spatially explicit, we indirectly consider the relative spatial arrangement of wolves through their pack affiliation and the equilibrium density parameter (Table 1).

The time step of the model is one year as the wolf life cycle is organized around reproduction that happens once a year. At each time step, all simulated individuals go through the same series of different sub-models representing different processes of the wolf life cycle, and each individual behaves differently according to its own characteristics. The first sub-models are, in order, reproduction, aging and mortality. They are followed by several sub-models related to changes in breeder/subordinate and resident/disperser status (Fig. 1). Most of the sub-models included in our IBM represent well-studied and well-quantified processes (Table 1). However, four processes of the wolf dynamics that we include are lesser known: the pack dissolution following the loss of a breeder, the adoption of young dispersing individuals by packs, the establishment of new packs using the budding strategy, and the different types of breeder replacement (Fig. 1). If the timing of pack dissolution, adoption and establishment by budding is fairly well understood, the intensity at which these processes occur in wolf populations has rarely been estimated. On the contrary, the timing of the different breeder replacement strategies is not well understood and still debated. We explore different parameter values for the sub-models pack dissolution, adoption, and new pack establishment by budding (Table 2), modifying the importance of the process in the wolf dynamics, and different timing (i.e., orders) for the sub-models concerning the breeder replacements (Fig. 1). Changing the relative order for the breeder replacement strategies induces a change in their relative importance as fewer packs are impacted by the final strategies as fewer packs are still missing a breeder.

2.1.3. Initial population

A wolf initial population is needed to launch the IBM simulations. The user specifies the composition of its initial population and its attributes, namely the equilibrium density, and immigration and emigration rates, to best represent the population he/she wants to model. Here is a simple example of the population we use in the following analyses. We build a fictive initial population of 10 packs and 5 dispersers, in an environment that can hold 30 packs in total (i.e., equilibrium density, Table 1). Specifically, the population comprises 5 packs of 2 breeders (5 years old each) with 2 pups (one male and one female); 3 packs of 2 breeders (5 years old each) with 1 yearling (male) and 1 pup (female); 2 packs of 2 breeders (5 years old each) with 1 adult (female, 3 years old); and 5 dispersers (3 females, 2 males, 2 years old each). We estimate the size of the area where the population is simulated as the number of packs at equilibrium density multiplied by the average territory size for wolf populations in the Apennines (104 km^2) (Mancinelli et al., 2018). This area is used to calculate wolf density in density-dependent processes. We allow connections of the simulated population with other non-simulated wolf populations via an immigration of 0, 1 or 2 external wolves per year inside the simulated population, and an emigration of 10% of the dispersing wolves from the simulated population outside of the study area. The parameters equilibrium density, number of immigrants arriving per year and proportion of dispersing wolves emigrating are randomly chosen. A modification of their values surely will change the projections of the population but the impact of these parameters on wolf populations are well understood and are therefore not explored further in this study.

2.1.4. Well-known processes of the wolf life cycle

We define as well-known processes wolf dynamics that are well documented and well understood. These processes are usually included in wolf IBMs (Chapron et al., 2016; Haight et al., 2002; Marucco and McIntire, 2010). When coding the sub-models to reproduce these processes, we have reliable estimates to parameterize and time them in our model.

2.1.4.1. Reproduction. We simulate that all packs with a breeding pair reproduce each year (Marucco and McIntire, 2010). We define the number of pups breeding pairs produce by sampling values in a Poisson distribution (Table 1) (Chapron et al., 2016). The sex of each pup is randomly defined as male or female with a 1:1 ratio (Marucco and McIntire, 2010; Sidorovich et al., 2007). Newborn pups are of age 0. Pups are residents, with the pack ID of their parents, bear their mother and father IDs, and are assigned a cohort ID equal to the year of the simulation during which they are born.

2.1.4.2. Aging. All individuals age one additional year in this sub-model. Pups of the year are now 1 year old, yearlings are 2 years old, and individuals of 3 years old enter the adult age class.

2.1.4.3. Mortality. We simulate seven different mortality rates (Table 1), according to various combination of age and residence status of the individuals, and total number of packs related to the number at equilibrium density. Mortality is applied individually using a Bernoulli distribution. At each time step, the mortality probability is sampled from a Normal distribution using the mean and standard deviation parameters (Table 1) associated to the different categories of individuals.

2.1.4.3.1. Mortality for non-dispersing individuals. We apply a

Table 1
Parameters used in the wolf IBM for the non-explored sub-models (see Fig. 1). Probabilities and rates are estimates for a yearly time step.

Parameter	Sub-model in which the parameter is used (see Fig. 1)	Explanation	Value	Reference
Mean litter size	Reproduction	Number of pups that go out of the female den. Mean used for a Poisson distribution to generate the number of pups produced by a breeding pair.	6.1	Sidorovich et al. 2007
Pup mortality	Mortality	Mortality probability for wolves in their first year of their life.	0.602	Smith et al. 2010
Yearling mortality	Mortality	Mortality probability for non-dispersing yearlings.	0.18 (sd = 0.04)	Marucco et al. 2009
Non density-dependent adult mortality	Mortality	Mortality probability for non-dispersing adults when the population is not at equilibrium density.	0.18 (sd = 0.04)	Marucco et al. 2009
Density-dependent adult mortality	Mortality	Mortality probability for non-dispersing adults when the population is at equilibrium density. Mortality probability is calculated using the density-dependent survival φ as: logit(φ) = a + (b*((popDens-c)/d))), where popDens is the population density per 1000 km^2	a = -1.196 b = -0.505 c = 53.833 d = 17.984	Cubaynes et al. 2014
Equilibrium density	Mortality; Establishment in pairs; Establishment by budding; Establishment alone	Maximum number of packs the environment within which the population is simulated can hold.	30	Defined by the user
Territory size	Mortality	Average territory size (in km^2) for wolves. Used to calculate the study area size with the equilibrium density to estimate wolf density through the model.	104	Mancinelli et al. 2018
Mortality of dispersing, non-adopted pups	Mortality	Mortality probability for individuals that dispersed as pups, following their pack dissolution, and that were not adopted by a pack during the year.	1	
Disperser mortality	Mortality	Mortality probability for dispersers (except individuals that dispersed as pups).	0.31	Blanco and Cortes, 2007
Dissolution probability for pack with 1 breeder left	Pack dissolution	Probability of dissolution for small packs that have only 1 breeding individual left in the pack.	0.258	Brainerd et al. 2008
Dissolution probability for pack with no breeders left	Pack dissolution	Probability of dissolution for small packs that do not have any breeding individual left in the pack.	0.846	Brainerd et al. 2008
Relatedness threshold	Replacement of breeding females by subordinates; Establishment in pairs; Establishment by budding; Replacement of breeders by dispersers; Replacement of breeding males by subordinates	Relatedness value between 1st cousins. Two individuals must have their relatedness coefficient less than or equal to this threshold to be considered unrelated.	0.125	Caniglia et al. 2014
Mean pack size	Dispersal; Adoption	Mean used for the Normal distribution to generate the sizes of each pack, representing their maximum pack size.	4.405 (sd = 1.251)	Marucco and McIntire, 2010
Pup dispersal probability	Dispersal	Relative probability (compared to the other age categories) for a pup to leave the pack and become disperser.	0.25	Haight and Mech, 1997
Yearling dispersal probability	Dispersal	Relative probability (compared to the other age categories) for a yearling to leave the pack and become disperser.	0.5	Haight and Mech, 1997
Adult dispersal probability	Dispersal	Relative probability (compared to the other age categories) for an adult to leave the pack and become disperser.	0.9	Haight and Mech, 1997
Number of immigrants	Immigration/ Emigration	Number of immigrants arriving in the population. All values have the same probabilities to be chosen.	0, 1, or 2	Defined by the user
Proportion of emigrants	Immigration/ Emigration	Proportion of dispersing individuals that emigrate outside of the study area.	0.1	Defined by the user

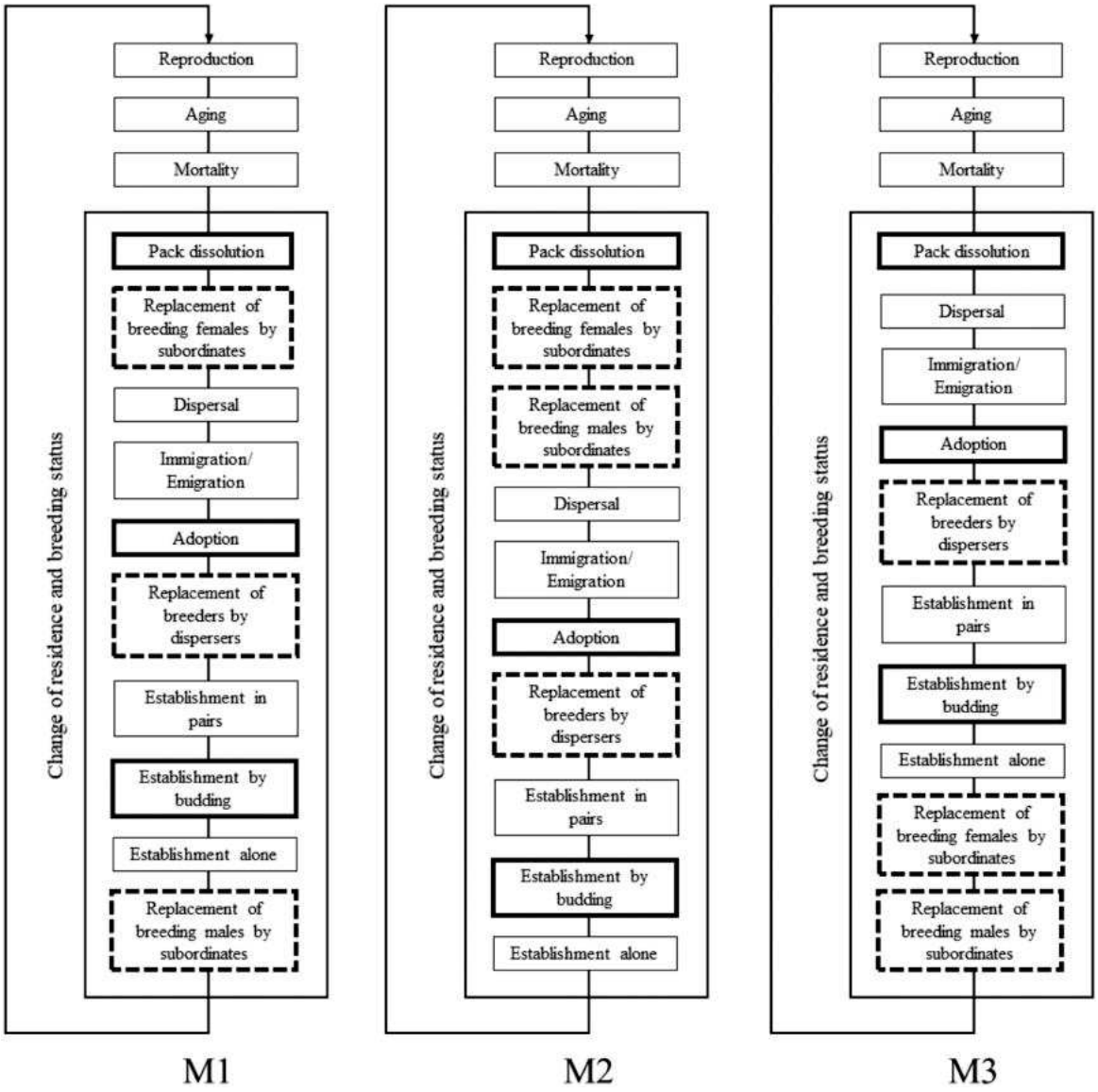

Fig. 1. Diagram of three different versions of the wolf IBM (M1, M2 and M3). The sub-models in solid bold boxes are the lesser-known processes explored with different parameter values (Table 2). The sub-models in dashed bold boxes are the lesser-known processes related to breeder replacement for which their order, instead of their parameter, is tested with the three versions of the sub-models series: M1, M2, and M3. When a wolf population is simulated with one of these model versions, individuals go through each sub-model of the loop all together, one sub-model at a time, for as long as the simulation lasts. The loop of sub-models represents a one-year time step.

Table 2
Parameters used in the wolf IBM for the explored sub-models (see Fig. 1). Probabilities are estimates for a yearly time step.

Parameter	Sub-model in which the parameter is used (see Fig. 1)	Explanation	Tested values
Pack size threshold for dissolution	Pack dissolution	Pack size to differentiate large and small packs. Packs with fewer individuals than this threshold are considered small and can dissolve if 1 or 0 breeding individual remains.	3.1; 4.1; 5.1
Probability of adopting	Adoption	Probability for a pack that has less member than its maximum pack size to adopt a young disperser.	0.1; 0.5; 0.9
Probability of budding	Establishment by budding	Probability of success for a disperser to establish a new pack by budding. This probability is multiplied by the density-dependent probability of establishment for the dispersers.	0.1; 0.5; 0.9

different probability of mortality for non-dispersing individuals regarding their age category (i.e., pups, yearlings or adults) (Table 1). To mimic density-dependence in adult mortality (Cubaynes et al., 2014), we apply two mortality rates for this age category depending on the number of packs established in the population during any given year of the simulation. If the number of packs is below the equilibrium density, mortality is fixed (Table 1). If the number of packs reaches equilibrium density, we linked wolf mortality with wolf density following Cubaynes et al. (2014).

2.1.4.3.2. Mortality for dispersing individuals. Dispersing yearlings in this sub-model are individuals whose pack dissolved in the previous year when they were pups and that were not adopted by any pack

during that year. Their likelihood of survival alone is low without food or care from adults or yearlings (Brainerd et al., 2008; Mech and Boitani, 2003) so we set their mortality probability to 1. Otherwise, we set the same fixed mortality to all dispersing adults (Table 1).

2.1.4.3.3. Mortality for old individuals. We do not model senescence or any increase in mortality rate with age. However, to represent a realistic age distribution in the population, we allow wolves to live up to their 15th year of age (Marucco and McIntire, 2010), and all individuals of this age die entering the successive year of simulation.

2.1.4.4. Dispersal. For each pack, and at each time step, we simulate the maximum number of individuals packs can support using a Normal distribution (Table 1). If a pack exceeds its simulated threshold, a certain number of individuals disperse until the number of wolves in the pack levels off at the threshold. While breeding individuals do not disperse, all other wolves can. Among these, the choice of dispersing individuals is based on relative probabilities related to their age category (Table 1).

2.1.4.5. Immigration/Emigration. According to the immigration portion of the sub-model, at each time step, a determined number of immigrants enters the population (Table 1). Immigrants are simulated as dispersers, generated from another wolf population. Their sex is randomly assigned (i.e., male or female with a 1:1 ratio), and their age is simulated using a truncated Poisson distribution bounded between 1 and 15 with mean equal to 2 as dispersers are most commonly yearlings (Mech and Boitani, 2003). Immigrants do not belong to any pack of the simulated populations yet, and consequently are not breeders. As they were born outside the simulated population, they do not hold information about their mother ID and father ID (i.e., they are unrelated to any other individuals). However, once immigrating, they behave the same way (i.e., follow the same sub-model rules) as the native wolves. For the emigration portion of the sub-model, a proportion of the current dispersing individuals (Table 1), randomly chosen, leaves the simulated population. These individuals do not come back and their disappearance is similar to simulating their death.

2.1.4.6. Pack establishment by breeding pairs. We define that reproductively mature male and female dispersers that are not closely related can pair bond, establish together as breeders, and form a new pack. The relatedness threshold chosen is that of the first cousins (Table 1); in wolves, breeding pairs are rarely more related than cousins, except when they have no other option (i.e., mating between siblings or parents and pups are generally avoided (Caniglia et al., 2014)). This relatedness threshold is the same for all sub-models. Establishment by breeding pairs is possible only if the number of existing packs has not yet reached equilibrium density. The density-dependent probability for dispersers to pair bond is defined by a Bernoulli distribution with probability equal to the number of packs that can be established until reaching equilibrium density divided by equilibrium density (i.e., the more packs there are, the less chance for dispersers to pair bond and establish new packs). Once a pair bond is established, both wolves become breeders and residents, sharing the same, new and unique pack ID.

2.1.4.7. Pack establishment by single wolves. If the area is not at equilibrium density, our model allows mature dispersers that did not pair-bond to establish a territory by themselves. Similar to establishing in pair, the probability to establish a territory alone is density-dependent. Single wolves holding the new territory become breeders (even if no reproduction is possible yet) and residents of a new pack (i.e., they are assigned a new and unique pack ID). Then, at the next time step, a mature disperser of opposite sex will be able to take the vacant breeding position and finally reproduce.

2.1.5. Lesser-known processes of the wolf life cycle

We define as lesser-known processes wolf dynamics that are known to occur in the wild but that are not extensively documented. These processes have not been included in previous IBMs for wolves (Chapron et al., 2016; Haight et al., 2002; Marucco and McIntire, 2010). When coding the sub-models to reproduce these processes, we do not have reliable estimates to parameterize or streamline them inside the life cycle available from the literature.

2.1.5.1. Pack dissolution. We simulate that small packs whose social structure is impacted by the loss of one or both breeders may dissolve with different probabilities regarding how many breeders remain (Table 1). In the specific case where both breeders die and only pups remain in a pack, we consider that the pack always dissolves, as pups are unlikely to maintain a territory by themselves. If these pups are not adopted during the current year, they die in the mortality sub-model during the next time step. When a pack dissolves, all former members of the pack become dispersers and do not belong to a pack anymore. Former breeding individuals also lose their breeder status. Brainerd et al. (2008) differentiate small packs, in which dissolution can occur following the loss of one or two breeders, from large packs in which dissolution never occurs. They do not define a threshold between small and large packs but estimate that small packs have on average 2.36 individuals and large packs 5.75. We explore the importance of the pack dissolution process on the wolf population dynamics by varying this pack size threshold differentiating small packs from large ones (Table 2). A small threshold induces that only very small packs can dissolve, therefore minimizing the influence of pack dissolution on wolf dynamics. A large threshold allow more packs to be concerned, hence maximizing the influence of pack dissolution on wolf dynamics.

2.1.5.2. Adoption. We define in our model that packs whose size is below their maximum threshold (estimated in the dispersal sub-model) can adopt as many individuals between 1 and 3 years old (inclusive) as allowed by their maximum pack size. Among potential adoptees, dispersing males are selected first. If there are no more males available to adopt, and packs are still small enough, then females are chosen next as adoptees. Once adopted, individuals become non-breeding (i.e., subordinate) residents and acquire their pack ID. Adoption has been observed (Mech and Boitani, 2003) but the rate at which this process occurs is unknown. To explore how relevant this process is to affect wolf population dynamics, we defined different probability values for a pack to adopt (Table 2).

2.1.5.3. Pack establishment by budding. Similar to the other strategies of establishment, budding is possible only if the number of packs in the population has not reached the equilibrium density. We define a density-dependent probability for a disperser to bud similar to the one of pack establishment through pair-bonding. Only mature dispersers can bud, and only with a non-breeding mature resident of the opposite sex that is not closely related (Table 1). Once budding occurs, both wolves that pair become breeders and residents, and obtain the same, new and unique pack ID. There are no detailed studies indicating how common budding is, compared to alternative ways of pack establishment. We explore the influence this process might have on wolf population dynamics by testing different probabilities of budding (Table 2) that we multiply to the density-dependence probability of pack establishment.

2.1.5.4. Replacement of missing breeders

2.1.5.4.1. Replacement of breeding females by subordinates. We select the subordinates to replace the missing breeding females by randomly choosing one of the subordinate mature females in the concerned packs. To mimic inbreeding avoidance in wolf packs, we then look at the relatedness between the chosen females and the current breeding males, if there is any. In case a breeding male is closely related to the

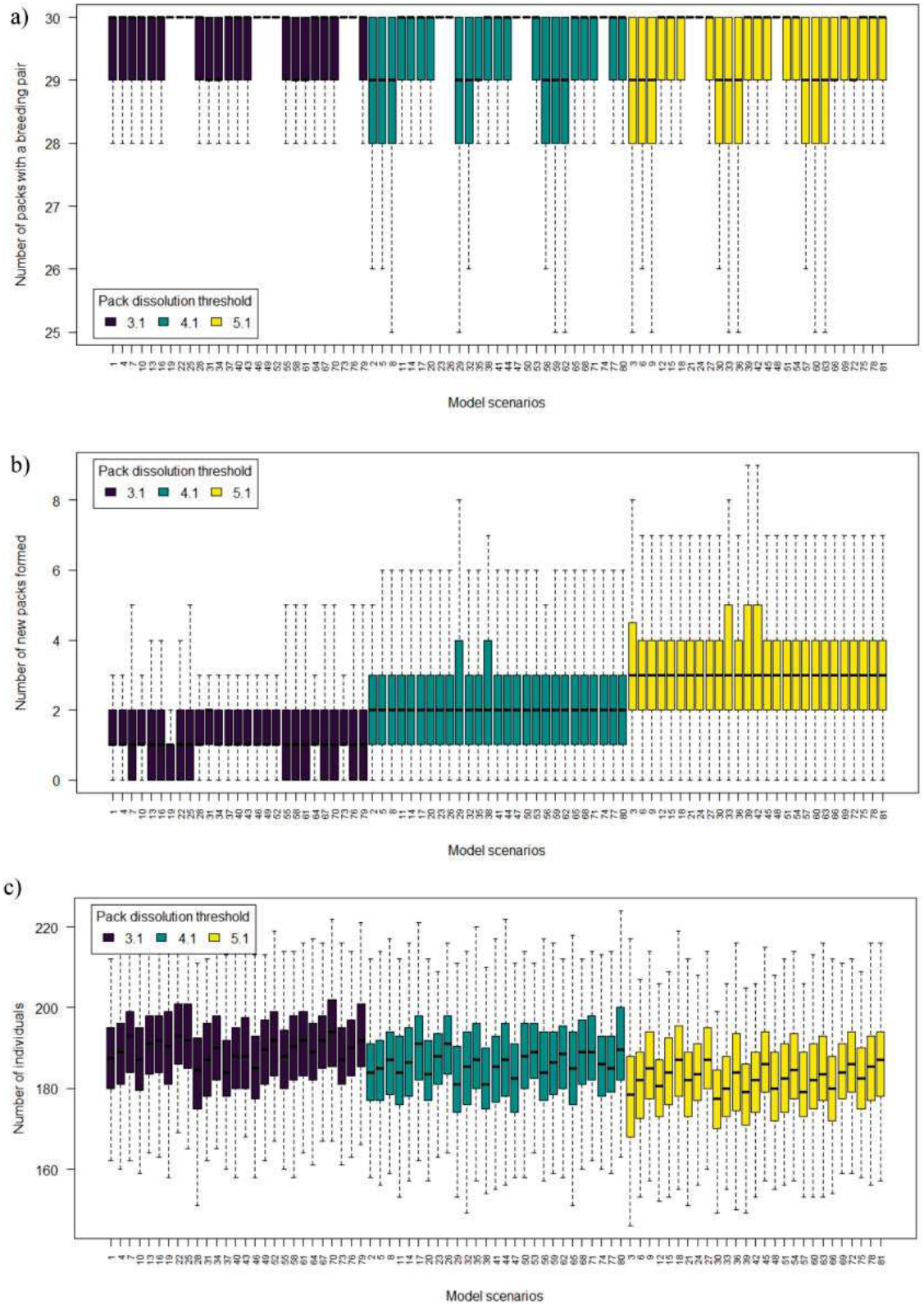

Fig. 2. Boxplots of model outputs, based on the parametrization of the pack dissolution sub-model: (a) number of packs with a breeding pair after the last year of simulation, (b) number of new pack created during the last year of simulation, and (c) total number of individuals in the population after the last year of simulation. Colors of the boxplots refer to the three pack dissolution thresholds that were tested (i.e., packs whose size is below may dissolve after the loss of one or both breeders; Table 2). 27 model scenarios were run for each threshold value (i.e., color), referring to different combination of parameters, for a total of 81 model scenarios (Appendix B). Boxplot values represent model outputs extracted from the 200 replicates of each model scenario.

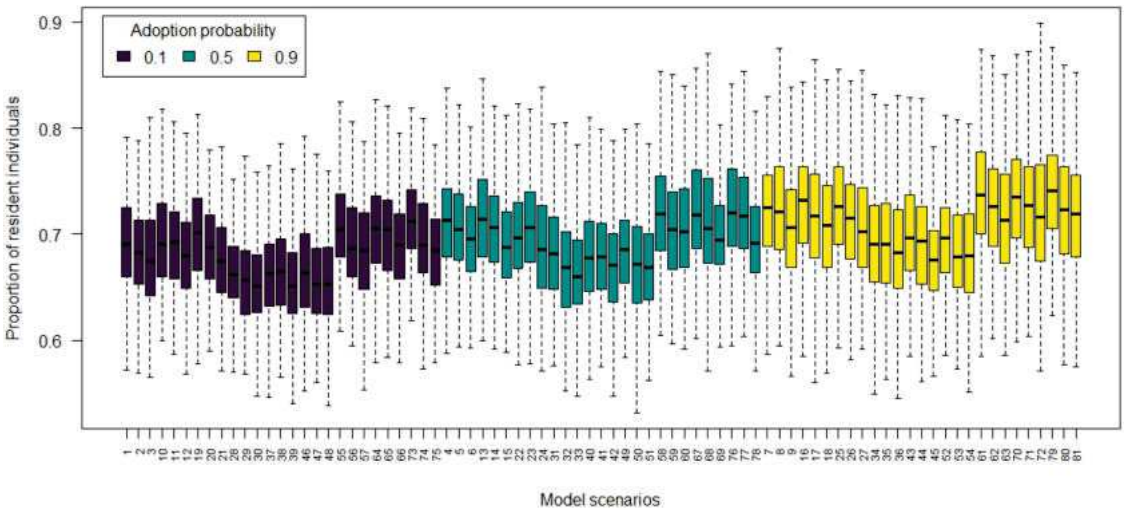

Fig. 3. Boxplot of model output, based on the parametrization of the adoption sub-model: proportion of resident individuals in the population after the last year of simulation. Colors of the boxplot refer to the three adoption probabilities that were tested (i.e., probability for a pack to adopt a disperser; Table 2). 27 model scenarios were run for each probability value (i.e., color), referring to different combination of parameters, for a total of 81 model scenarios (Appendix B). Boxplot values represent model output extracted from the 200 replicates of each model scenario.

female (Table 1), he may be replaced by a less related subordinate or a disperser (in sub-models *2.1.5.4.2. Replacement of breeding males by subordinates*, or *2.1.5.4.3. Replacement of breeders by dispersers*). We explore how the alternative sequence of the breeder replacement sub-models (i.e., breeders replaced by subordinates followed by breeders replaced by dispersers, or vice versa, independently for each sex; Fig. 1) affect projections of wolf population dynamics.

2.1.5.4.2. Replacement of breeding males by subordinates. If there are several mature male subordinates in the pack where the male breeding position is vacant, the least related to the current breeding female, if there is any, is chosen to become breeder. If there are several unrelated subordinate males, or if there is no breeding female, one is selected randomly. In the case where the breeding female is related to the newly chosen breeding male but there is a mature female subordinate less related, the latter usurp the breeding female and the former breeding female is dismissed (i.e., becomes subordinate). If there are several unrelated mature female subordinates, one is selected randomly. We add that, in the particular case where a pack was not missing a breeding male but the breeding female obtained her breeding status during the time step (in *2.1.5.4.1. Replacement of breeding females by subordinates*) and she was too related to the current breeding male, one of the less related male subordinates can take over the male breeding position in this sub-model. All of these rules mimic inbreeding avoidance in wolves, except when there is no other choice to reproduce (Mech and Boitani, 2003). Once new breeding individuals are chosen, they will be able to mate the next year.

2.1.5.4.3. Replacement of breeders by dispersers. Here, we simulate the replacement of all missing breeders, both females and males, by mature dispersers. First, missing breeding females are replaced by mature dispersing females, unrelated to the current breeding males in the packs if there is any. Then, missing breeding males are replaced similarly. Selected dispersers thus become breeders of packs, resident and acquire the ID of the pack they joined.

2.2. Model scenarios tested

We explore the impact of the four lesser-known processes on wolf population projections by varying and combining their different parameters values (Table 2) or timing (Fig. 1), resulting in 81 model scenarios (Appendix B). We run 200 replicates of each scenario for a 25-year simulation period, starting with the same initial population and same parameters for the well-known processes (Table 1).

2.2.1. Model outputs

For each simulation, the complete population with the individual's characteristics is available for each simulated year. The change in pack numbers is also recorded after each event potentially modifying their number: individual mortality (i.e., if all members of a pack die), pack dissolution, and the three types of new pack establishments. We derive, from the model outputs, six metrics that we consider crucial to evaluate wolf conservation and management. Specifically, we calculate, for each simulated year and for each replicate of each model scenario, the number of packs with a breeding pair. Then, we extract 1) at which year populations reach equilibrium density. This output represents the speed of the population expansion and is a key element in areas that are being recolonized by the wolf. All the other metrics are defined using model outputs extracted after the last year of simulation, once all populations are at equilibrium density. We calculate for each replicate of each model scenario: 2) the number of packs with a breeding pair, as this corresponds to the reproductive potential of the population and is of importance for management issues related to population growth. 3) The number of packs newly established during the final year. This represents the pack turnover and the stability of the population that may affect mortality compensation, species expansion, or wolf-human conflicts (e.g., new packs may be more or less prone to attack livestock compared to old-established packs which know the associated risks and benefits). 4) The abundance of the population (i.e., total number of individuals) and 5) the proportion of residents and dispersers in the population. Population size is often required in management, and knowing the relative proportions of residents vs dispersers may help in understanding the demographic and social performance of the population and its potential to further expand its range. Finally, we compute 6) the relatedness between the two breeders in each pack. Inbreeding avoidance plays a big part in the wolf life cycle, affecting the replacement of the missing breeders and the creation of a new pack.

2.3. Sensitivity analysis

We run a sensitivity analysis on the parameters of the well-known processes (Table 1) to identify if some may influence the conclusions on the lesser-known processes. We use the model version M1 as a plausible model version, and the parameter values 4.1, 0.5, and 0.5 (i.e., all intermediate values) for the parameters of the sub-models pack dissolution, adoption and establishment by budding respectively. We run this model modifying the parameters of the well-known processes (Table 1)

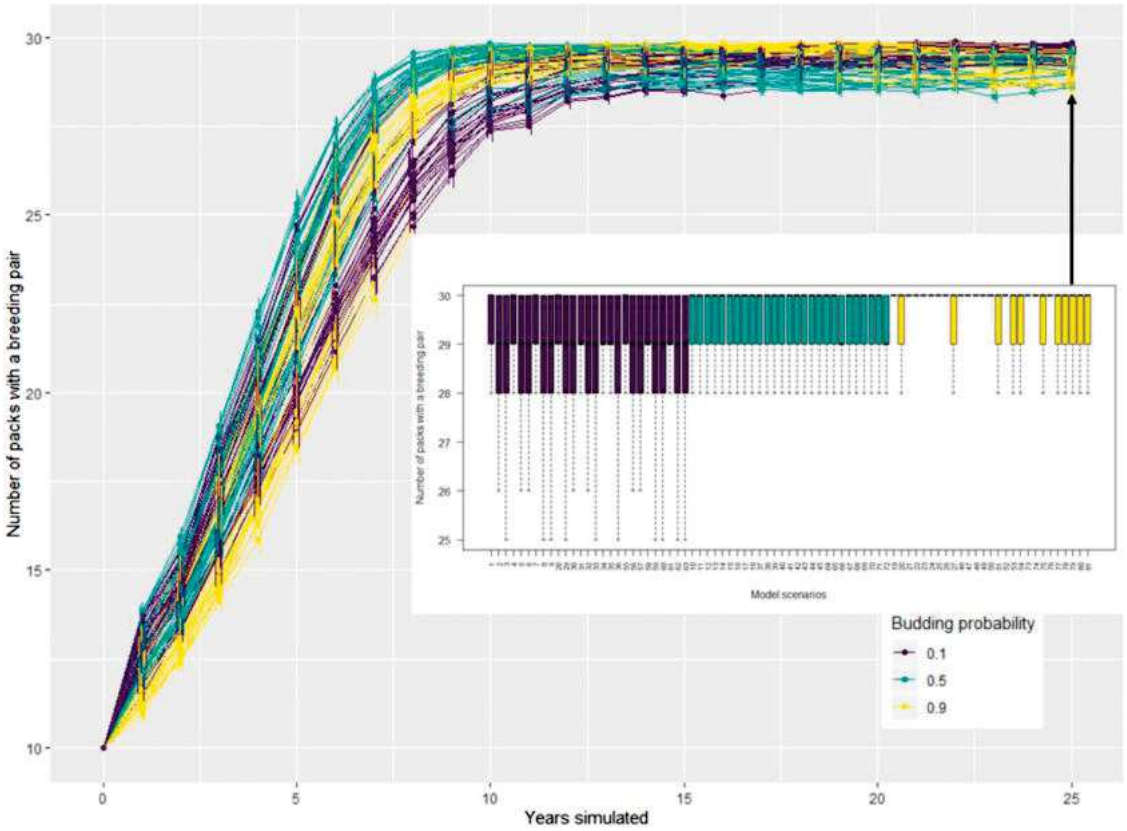

Fig. 4. Model outputs based on the parameterization of the pack establishment by budding sub-model: time at which populations reach equilibrium density (lines) and number of packs with a breeding pair after the last year of simulation (boxplot). Colors of the lines and boxplot refer to the three probabilities of establishment by budding that were tested (Table 2). 27 model scenarios were run for each probability value (i.e., color), referring to different combination of parameters, for a total of 81 model scenarios (Appendix B). Lines represent the mean values and their 95% confidence intervals, per year, from the 200 replicates of each model scenario. Boxplot values represent model output extracted after the last year of simulation from the 200 replicates of each model scenario. A larger figure of the boxplot is available in Appendix C.

one parameter at a time by either increasing or decreasing its value by 5% (Ovenden et al., 2019). We run 200 replicates of the model over 25 years to test each parameter. The model is considered sensitive to a parameter if a model output (i.e., mean value over the 200 replicates) with a modified parameter varies more than 20% from the original results (Kramer-Schadt et al., 2005; Ovenden et al., 2019). We examine the six model outputs described above in the *2.2.1. Model outputs* section. We do not test the sensitivity of the model to standard deviation parameters (standard deviation of mortality and of pack size, Table 1). Regarding the density-dependent mortality function, we only test the sensitivity of the slope parameter and do not test the sensitivity to the intercept and to the parameters standardizing the population density (Table 1).

2.4. Model implementation

The IBM is coded in R 3.5.2 (R Core Team, 2014). We use the R package *NetLogoR* (Bauduin et al., 2019) to facilitate the implementation of the individual-based model structure in R language and the package *pedantics* (Morrissey, 2018) to calculate relatedness between individuals using their mother and father IDs. We use the packages *SciViews* (Grosjean, 2018) for the logarithms functions and *testthat* (Wickham et al., 2019) to implement tests in our model and verify the outcomes of the sub-models. The R files to run the model are available in the GitHub repository (https://github.com/SarahBauduin/appendix_wolfIBM) under the GNU General Public License v3.0.

3. Results

3.1. General results for the wolf IBM

Figures showing all model outputs for the 81 model scenarios are presented in Appendix C. All scenarios project a growth of the wolf population. Starting from 10 packs and 43 wolves, after 25 years of simulation populations reach a mean of 29.4 packs (sd = 1.0) with a breeding pair, for an overall mean population size of 186.2 wolves (sd = 12.4). In all model scenarios, populations stabilize and reach equilibrium density after about 10 years of simulation (mean = 9.8 years, sd = 2.8).

3.2. Effect of lesser-known social processes on wolf dynamics

We only present model outputs that show an impact from the parameterization or timing of the explored sub-models. Values reported are means and standard deviations calculated from all replicate simulations from each set of 27 model scenarios with the same parameter value or model version for the explored sub-model (i.e., 3 parameters or model versions * 27 model scenarios = 81 total).

3.2.1. Pack dissolution

The different parameter values for the pack dissolution threshold influence the number of packs with a breeding pair and the total number of individuals in the population after the last year of simulation, as well as the number of new packs formed during the last year of simulation. Model scenarios where only small packs (i.e. with 3 individuals or less) may dissolve after breeders loss project wolf

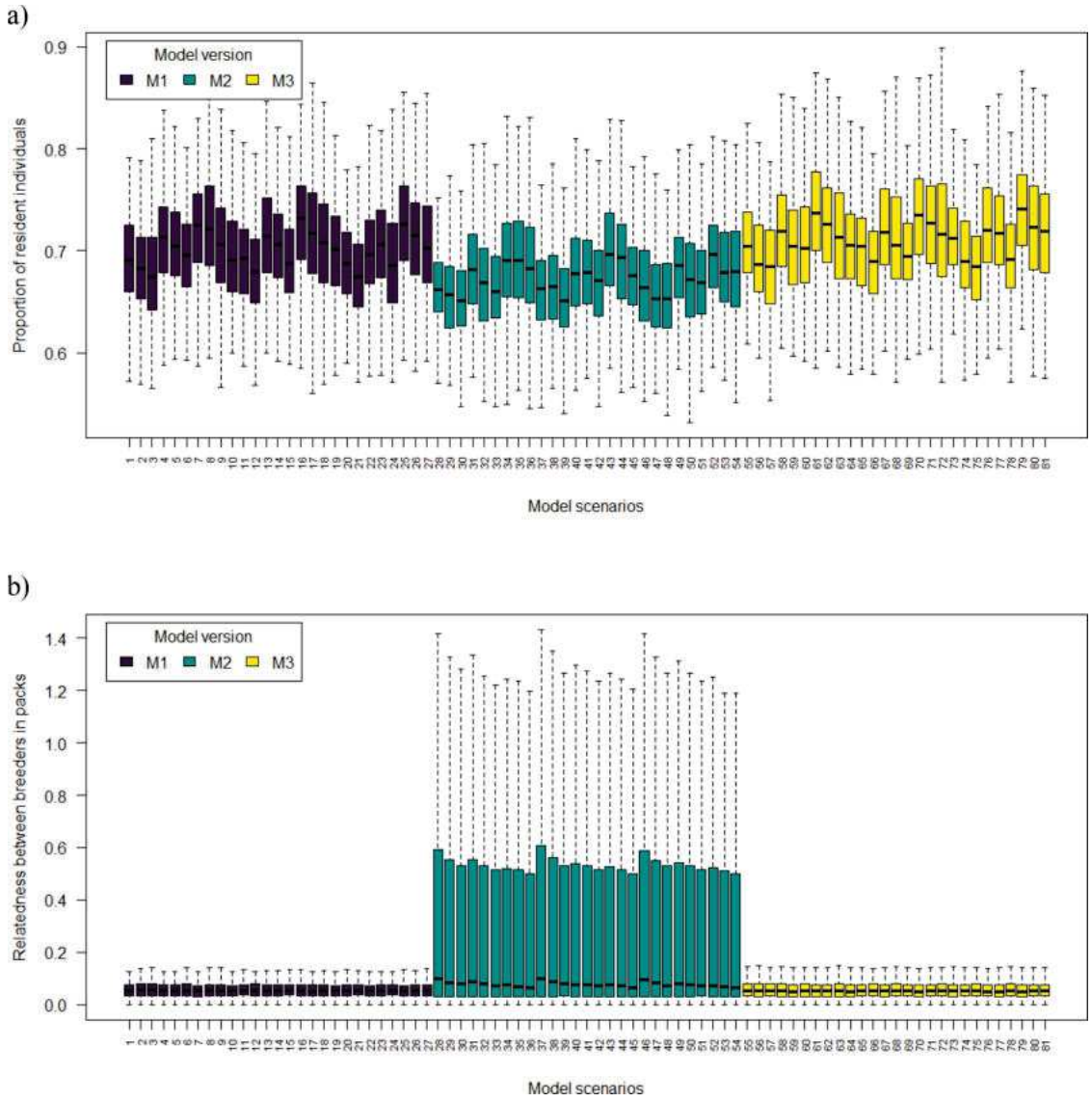

Fig. 5. Boxplots of model outputs, based on the timing of the different sub-models simulating the replacement of missing breeders: a) proportion of resident individuals in the population after the last year of simulation, and b) relatedness value between the male and female in breeding pairs after the last year of simulation. Colors of the boxplots refer to the three model versions representing different orders for the breeder replacement strategies that were tested (i.e., relative order of the breeder replacement by subordinates and by dispersers; Fig. 1). 27 model scenarios were run for each model scenario (i.e., color), referring to different combination of parameters, for a total of 81 model scenarios (Appendix B).Boxplot values represent model outputs extracted from the 200 replicates of each model scenario.

populations with on average 29.6 packs with a breeding pair (sd = 0.8). Scenarios where larger packs may dissolve (i.e., packs up to 4 and up to 5 individuals) project on average 29.4 packs (sd = 1.0), and 29.2 packs (sd = 1.1) respectively (Fig. 2.a). The most impacted model output by this sub-model parameterization is the number of new packs formed during the last year of simulation. More new packs are formed as larger packs are allowed to dissolve: with the threshold values 3.1, 4.1, and 5.1, the mean number of new packs created are equal to 1.3 (sd = 1.1), 2.2 (sd = 1.5) and 3.2 (sd = 1.7) respectively (Fig. 2.b). Regarding the number of individuals in the populations, the averages are equal to 189.4 (sd = 11.9), 186.3 (sd = 12.1), and 182.8 (sd = 12.3) respectively (Fig. 2.c).

3.2.2. Adoption

The different parameters for the adoption sub-model seem to only mildly influence the proportion of resident individuals in the populations. With an adoption probability set to 0.1, model scenarios project on average 68.1% of the population being resident (sd = 5.9%), with an adoption probability equal to 0.5, the result is of 69.7% (sd = 5.4%) and with an adoption probability equal to 0.9, the result if of 71.2% (sd = 5.8%) (Fig. 3). The impact of varying the adoption probability from 0.1 (i.e., almost no adoption occurring) to 0.9 (i.e., adoption happening very often when possible) is very low on this model output and non-existent on the other ones (Appendix C).

3.2.3. Pack establishment by budding

The model outputs the most impacted by the different parameter values for the probability of establishment by budding are the time at which populations reach equilibrium density and the number of packs with a breeding pair at the end of the simulation. The lowest probability of budding (i.e., equal to 0.1) project wolf populations reaching the equilibrium density the latest, on average after 11.8 years of simulation (sd = 3.0) (Fig. 4). With the budding probability equal to 0.5, populations reached that point on average after 9.6 years (sd = 2.2) (Fig. 4). With the highest probability of budding (i.e., equal to 0.9), populations reach the equilibrium density the fastest, on average after 8.2 years of simulation (sd = 1.7) (Fig. 4). The observed differences in numbers of packs after the last year of simulation follow the same patterns: the

highest budding probability produced the highest mean values. Model scenarios with a budding probability equal to 0.1 project wolf populations with on average 29.0 packs (sd = 1.2), with a probability of 0.5, there are on average 29.4 packs (sd = 1.0), and with the budding probability equal to 0.9, there are on average 29.7 packs (sd = 0.6).

3.2.4. Replacement of missing breeders

The model versions testing the different timing of sub-models concerning breeder replacement influence mildly the proportion of resident individuals in the population after the last year of simulation, but it greatly impacts the relatedness value between male and female in breeding pairs. Model versions M1 and M3 have similar results, and they both differ compared to those obtained using M2. M1 (Fig. 1) with the replacement of missing breeding females by subordinates first and the replacement of missing breeding males by dispersers first, project populations with a mean proportion of resident equal to 70.3% (sd = 5.3%) (Fig. 5.a). It is similar to M3 (Fig. 1) where the replacement of missing breeders was done primarily by dispersers for both sexes; projected populations have on average 71.2% of resident individuals (sd = 5.5.%) (Fig. 5.a). In M2 (Fig. 1) where the replacement of missing breeders was done primarily by subordinates, projected populations have on average 67.5% of resident individuals (sd = 5.1%) (Fig. 5.a). The influence of the different model versions is greater on the relatedness between breeders. For M1, the mean relatedness is equal to 0.06 (sd = 0.03), similarly as for M3 (mean = 0.06, sd = 0.04). For M2, it is equal to 0.26 (sd = 0.31) (Fig. 5.b). M1 and M3 favor the replacement of at least one missing breeder by a disperser and keep relatedness between breeders very low. In M2, missing breeders are primarily replaced by subordinates and mating between related individuals frequently occur.

3.3. Sensitivity analysis

As expected, the parameter affecting the most model outputs, apart from the ones tested for the lesser-known processes, is the equilibrium density. The number of new packs created is sensitive to this parameter. All the other model outputs are slightly sensitive to the equilibrium density parameter but not in the range of [- 20%; + 20%]. Pup mortality is the second parameter affecting the most model outputs but none vary more than the range of [- 20%; + 20%]. Overall, the six model outputs we look at are not sensitive to the parameters of the well-known processes (Table 1). The complete table with the value tested for the parameters and the results for the model outputs is available in Appendix D.

4. Discussion

We developed an IBM to represent wolf demography and pack dynamics while exploring lesser-known processes of the species social dynamics. We explored different parameterization and timing for the processes of pack dissolution, adoption, establishment by budding, and replacement of missing breeders. Although the effects on the model outputs were relatively small, the projections from the different model scenarios pointed out the importance of the pack dissolution, establishment by budding and replacement of missing breeders processes in wolf population projections. Further research is needed to better understand these processes and the mechanisms behind, to be able to correctly incorporate them in the IBM with reliable parameter values and timing among the different sub-models. Among these three processes, the different orders of the breeder replacement strategies produced the largest effect on the breeder relatedness; this process should be the first focus of attention for more investigation. The fourth studied process (i.e., adoption) did not modify much the model outputs, possibly indicating a lesser influence of this process on wolf dynamics.

Our model also innovatively accounted for relatedness between individuals and density-dependence. Adding a genetic component to our model is especially important to investigate hybridization and inbreeding depression that can be of great concern for wolf management and conservation (Bohling and Waits, 2015). Our analyses also highlighted the modularity and flexibility of our IBM that can be adapted and used by ecologists to explore various questions and test different hypotheses on wolf ecology, management, and conservation.

To explore the process of pack dissolution, we tested different values for the pack dissolution threshold to allow more or less packs to dissolve, given different importance to this process in the wolf dynamics. Diminishing the importance of pack dissolution produced populations often being at equilibrium density with few new packs created, mimicking a very stable population. The other way a pack can disappear, except than by dissolution, is by the death of all its members at once, which rarely happened in the simulations. On the contrary, allowing more packs to dissolve reduced the number of packs, freed space and partners to create new packs, and therefore favored the pack turnover. Still, the creation of new packs did not seem to reach the same intensity as the one of pack loss, as the final number of packs and individuals were slightly lower when pack dissolution was important. However, pack dissolution influenced more the composition of the packs at the individual level (i.e., pack turnover impacted) than the projections at the population level (e.g., total number of packs and individuals). This is in agreement with a study by Borg et al. (2015) showing that with or without pack breaking down following breeder losses, the overall dynamics of the population was quite similar (e.g., number of packs), highlighting a compensation mechanism. On the other hand, population stability is a key element in social species where individual personalities and group compositions matter, such as regarding hybridization (Bohling and Waits 2015) and depredation (Allen, 2014), as well as their associated management actions. This process requires more field investigations to better understand the conditions leading to pack dissolution. Its understanding and inclusion in model would be rather relevant when individual identity is important (e.g., hybridization).

Budding is a strategy to establish and create new packs. With a low probability to bud, less packs are created and, as expected, simulations with the smallest probability of budding projected populations which were the slowest to reach equilibrium density. Inversely, maximizing the importance of budding projected populations reaching equilibrium density the fastest. At the end of the simulation, when the populations were at equilibrium density, the same pattern occurred with the more the budding strategy was used, the more packs were present in the populations. However, the different budding probability only slightly influenced the number of packs when the population was at equilibrium density. A better understanding of this process seems relevant to understand its relative importance regarding the other strategies of establishment to produce reliable projections, especially during the growing phase of the population. Therefore, this strategy of establishment is important to be understood and considered when the studied populations are in their colonizing phase.

Having the replacement of the missing breeding female by a subordinate first (M1) has been documented in some study sites (Caniglia et al., 2014; Jedrzejewski et al., 2005; Vonholdt et al., 2008) but the regularity of this behavior is debated. The modified model version where the replacement of the missing female breeder was done by a disperser before (M3) produced very similar model outputs. However, the model version where both missing breeders were replaced by subordinates first (M2) produced very different projections for the relatedness between breeders, and to a lesser extent on the proportion of resident individuals in the population. If we consider a breeding pair related when their relatedness coefficient is larger than 0.125 (Caniglia et al., 2014), only 0.8% of the breeding pairs were related in populations projected with model versions M1 and M3. In contrast, 38.1% of the breeding pairs were related in populations projected by M2. VonHoldt et al. (2008) evaluated that 7% of the breeding pairs in the Yellowstone grey wolf population were related. The difference in

our projections and the value found by VonHoldt et al. can be due to spatiality. In our model versions M1 and M3, all dispersers are available to replace missing breeders, hence reducing the risk of inbreeding. In the wild, dispersers can be too far away and therefore not available to the packs missing breeders, hence inducing a replacement of the missing breeders by subordinates and inbreeding. Understanding the functioning of the different types of breeder replacement and their timing is crucial seeing their impact on model projections. Studies on wolf genetics (e.g., inbreeding, hybridization) could conclude completely differently if using one or another model version, potentially inducing detrimental management recommendations for small isolated populations if projections were not reliable. The modular and flexible construction of our IBM model can allow future users to organize the replacement of the missing breeders in the order best representing their population of interest or the latest findings in literature.

Reducing the relative importance of the adoption process projected a higher proportion of dispersers as young wolves cannot be adopted by packs and therefore they remained floaters in the population (i.e., considered as "dispersers" in the model). The projected populations had more resident individuals when the adoption process was more important. This process seems the one influencing the least our model outputs. However, we selected general model outputs to best represent the conservation state of the wolf populations, and this process may influence other elements of the wolf population that we missed (e.g., sex ratio of subordinates in packs). Projecting population with a reliable number of resident and dispersing individuals can be of high importance when modeling demographic processes where dispersers and floaters have a main role such as the colonization of new areas (e.g., Boyd et al., 1999, Pletscher et al., 1997).

One of the limitations of our IBM approach is that it is non-spatial. This greatly simplifies the use and the adaptation of the model to other populations as no animal-environment interactions are modeled and therefore no data regarding these interactions, which are sometimes hard to acquire, are needed. Parameters like equilibrium density, territory size, number of migrants and proportion of emigration that need to be defined by the user give one way to account for spatial constraints given by a particular environment, and these parameters can be changed to best represent the study area of interest. That said, we acknowledge that an explicit spatial mechanism would be very interesting to implement as wolf pack occupancy is mainly driven by exclusive territoriality (Cassidy et al., 2016), but the population division and affiliation into packs approximated spatiality in our model. To add more spatial constraints without changing the model structure, a new individual characteristic could be defined to represent distances between individuals based on their pack affiliation. Individuals from the same pack would be closer to each other than to other individuals, allowing a researcher to define short-distance dispersers vs long-distance dispersers (Louvrier et al., 2018), separate from the immigration/emigration process of our model. With a bit more work, the model could be turned into a spatially explicit IBM by including an explicit dispersal sub-model like that in Marucco and McIntire (2010) in place of the current dispersal sub-model. Model outputs were sensitive to only a few parameters, apart from those linked to the explored processes. Equilibrium density naturally affected the model projections as this parameter represents, as stated above, one of the main spatial constraints influencing the simulated populations. This parameter triggered density-dependent events that occurred only when the landscape was fully occupied. Having more variability to trigger these events could likely reduce the influence of the equilibrium density parameter on model outputs and reduce the subjectivity of this trigger.

Building this IBM, we aimed to include all biological processes documented in the literature to best represent the wolf life cycle. Overall, we hope that our reproducible implementation of a modular and flexible IBM will contribute to the understanding, management and conservation of wolf populations by providing a scenario-testing and decision-making tool for ecologists and stakeholders, as well as a base model that can be adapted to simulate other canids and social species. The R language we used to code our IBM is largely used by ecologists and this should likely ease the model understanding and adaptation. For example, without much modification, our model could easily reproduce the life cycle of North American wolf populations with a few changes to the parameter values and the addition of a sub-model representing pack splitting (Jedrzejewski et al., 2004; Mech and Boitani, 2003). Users could also test hypotheses regarding assortative and disassortative mate choice for particular traits, relevant in hybridization studies (Fredrickson and Hedrick, 2006). Management actions (e.g., culling, sterilization) can as well be included in the model to test their effectiveness (Haight and Mech, 1997). The modular structure of our IBM allows the addition, removal or modification of only specific components of the model while keeping the other sub-models and the main structure the same. This model could be useful to other ecologists who could adapt it for their own specific research and management applications.

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Declaration of Competing Interest

None.

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Appendix A

Complete description of the wolf individual-based model (IBM) following the Overview, Design concepts, and Details protocol ("ODD" protocol) developed by Grimm et al. (2006, 2010).

Overview

Purpose

The wolf IBM aims to represent all non-spatial dynamics that happen in a wolf population, with a focus to detail pack dynamics, the change of status between disperser and residents, and the replacement of breeding individuals. The model also explores lesser-known processes of the wolf dynamics, namely: the pack dissolution following the loss of a breeder, the adoption of young dispersing individuals by packs, the establishment of new packs using the budding strategy, and the breeder replacement. These processes are known to happen in wolf populations but were rarely included in models (Marucco and McIntire 2010, Chapron et al. 2016; Pitt et al. 2003) due to the difficulty to parameterize or time them as little details are known on these processes. Other processes, better understood but also often over looked in models were also included: avoidance of inbreeding in packs where mating between wolves more related than two cousins is prevented as much as possible, density-dependent mortality for resident adults when the population is at equilibrium density, and movement of wolves in and out of the simulated population with possible immigrations and emigrations.

Entities, state variables, and scales

Entities in the model are wolf individuals. Each wolf has a unique ID, a sex (male or female), an age, a residence status (i.e., resident belonging to a pack or disperser), a pack ID if it belongs to a pack, a breeding status (i.e., breeding individual or not), a mother ID, a father ID, and a cohort ID (i.e., the year individuals are born in). ID, sex, mother ID, father ID and cohort ID never change during simulations. Age is updated each year. Residence status and pack ID change when an individual leaves or joins a pack. Breeding status changes when an individual becomes a breeder, either by replacing a missing one or by forming its own pack, or when an individual loses its breeder status after being replaced or after its pack broke apart. Packs are not considered entities in the model as most of the processes do not act on the whole pack at once (except pack dissolution). Packs are just a characteristic (via their ID) of the wolves. The model is non-spatial so the environment is not represented and wolves do not have a location. Temporal scale is a one-year time step.

Process overview and scheduling

In one year, all individuals go through the same series of sub-models (Fig. A1) and their state is modified according to the behavioral rules of each sub-model and their own characteristics. In order, these sub-models are: reproduction, aging, mortality, and change of resident/disperser and breeder/non-breeder status (Fig. A1). The change of the wolves' residence and breeding status is represented with several sub-models that are: pack dissolution, replacement of breeding females by subordinates, dispersal, immigration/emigration, adoption, replacement of breeders by dispersers, establishment in pairs, establishment by budding, establishment alone, and replacement of breeding males by subordinates (Fig. A1). The order of the sub-models simulating breeder replacement is debated and therefore is explored through different model versions (M1, M2 and M3, Fig. A1). For simplicity, the order used to present the model in the ODD is the one of M1 (Fig. A1) but we do not state that this model version is more reliable than the other ones. In "reproduction," new individuals (pups) are produced. In "aging," the age of all individuals is updated. In "mortality," different mortality probabilities affect different individuals based on their age, their residence status, and the number of existing packs relative to the equilibrium density. In "pack dissolution," some packs dissolve based on the age composition in the pack, their number of individuals and of breeders. If some packs dissolve, the residence status of the individuals is updated to dispersers and they lose their pack ID. In "replacement of breeding females by subordinates," female subordinates may replace the missing breeder in a pack and their breeding status is updated. In "dispersal," packs with too many individuals force some individuals to leave the pack with different relative probabilities based on their age. These individuals have their residence status updated to dispersers and they lose their pack ID. In "immigration," wolves from outside integrate into the population. In "emigration," wolves from the simulated population leave the study area; similar to death, they are removed from the population. In "adoption," young dispersing individuals may be adopted by small packs. These adoptees have their residence status updated to resident and they obtain the pack ID of their adopting pack. In "replacement of breeders by dispersers," dispersing individuals may replace missing breeders in packs. These individuals have their residence status updated to resident, they obtain the pack ID they integrate and their breeding status is updated. In "establishment in pairs," two dispersing individuals of the opposite sex establish themselves together to form a new pack. These individuals have their residence status updated to resident, they obtain a new and unique pack ID and their breeding status is updated. In "establishment by budding," a dispersing individual and a subordinate from a pack establish a new pack. The former disperser has it residence status updated to resident, it obtains a new and unique pack ID and its breeding status is updated. The former subordinate obtains the same pack ID as its new partner and has its breeding status updated. In "establishment alone," dispersers can establish themselves and form a pack alone. These individuals have their residence status updated to resident, they obtain a new and unique pack ID and their breeding status is updated. In "replacement of breeding males by subordinates," male subordinates may replace the missing breeder in the pack so their breeding status is updated. At the end of the sub-model series, the information about the current population (i.e., the current characteristics of each individual) is saved and individuals go through the same loop of sub-models for as many years as simulated.

Design concepts

Basic principles

The life cycle of the wolf is represented through the reproduction, mortality, dispersal and establishment of the individuals, already defined in published wolf IBMs (Marucco and McIntire 2010, Chapron et al. 2016). However, extensive research in the literature has been done to understand, and then include in the IBM, all processes known to happen in wolf dynamics. Additionally to the fundamental processes, we included those related to the change of status between residents and dispersers, the access to the breeding status, the pairing between male and female breeders based on their relatedness and the residence and breeding status, the movement of wolves in and out of the population, and density-dependent processes. The model provides new details on the pack dynamics to mimic the gray wolf life cycle as best as possible. The model is non-spatial but the spatial distribution of individuals is represented through their pack affiliation. The life cycle represented in the IBM as well as the parameter values used are more adapted to wolf populations in central Europe (i.e., Alps) than for large North American populations (i.e. Canada, Alaska (USA)).

Emergence

Through reproduction and immigration, new individuals are added in the population. Individuals die and are removed from the population

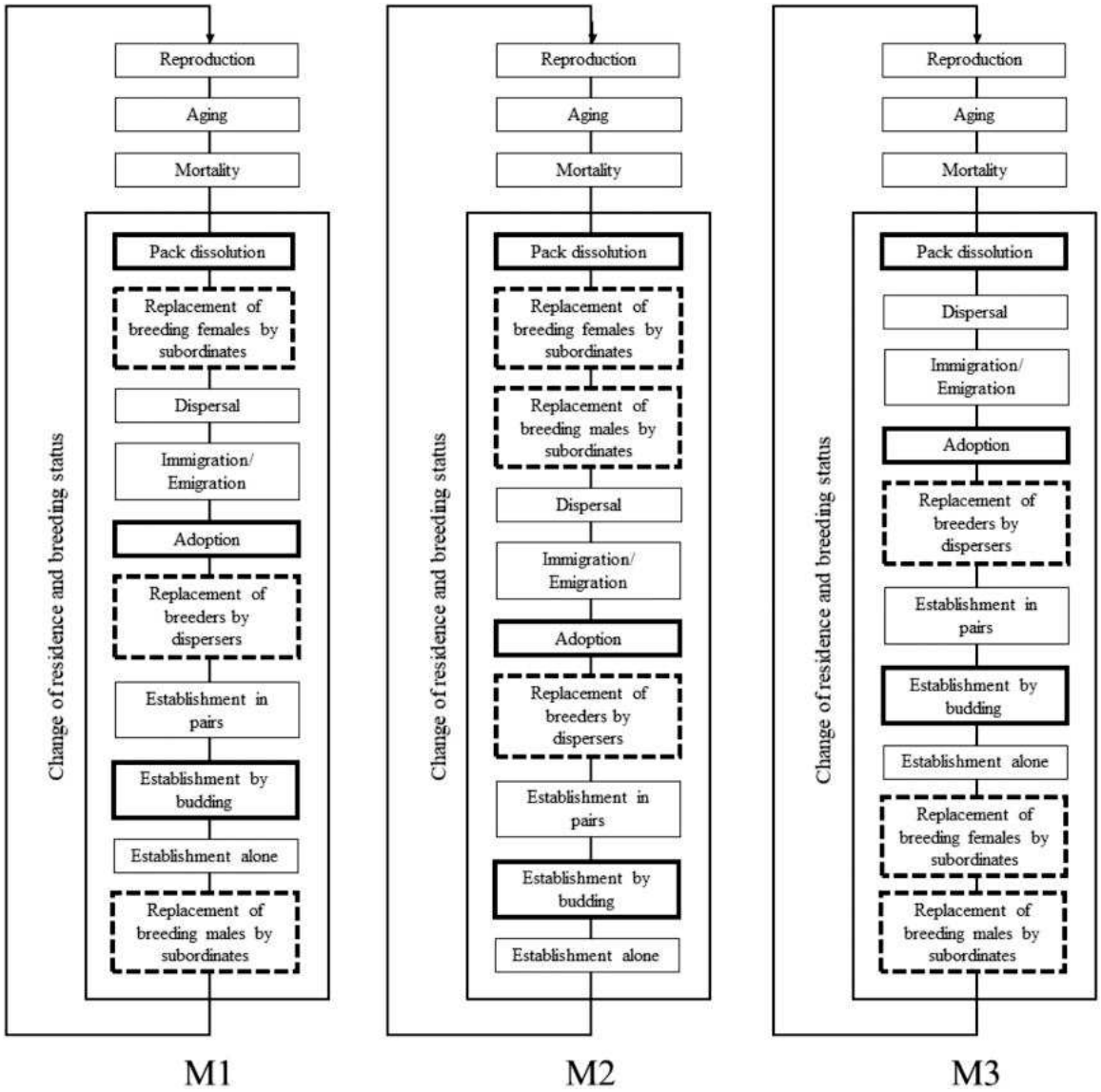

Fig. A1. Diagram of three different versions of the wolf IBM (M1, M2 and M3). The sub-models in solid bold boxes are the lesser-known processes explored with different parameter values. The sub-models in dashed bold boxes are the lesser-known processes related to breeder replacement for which their order, instead of their parameter, is tested with the three versions of the sub-models series: M1, M2, and M3. When a wolf population is simulated with one of these model versions, individuals go through each sub-model of the loop all together, one sub-model at a time, for as long as the simulation lasts. The loop of sub-models represents a one-year time step.

through different mortality and emigration processes. These changes in the population affect the total number of individuals. Processes affect wolves depending on their individual characteristics (i.e., age, sex, residence status, breeding status, etc.) and affect the distribution of the individuals in different classes (e.g., number of residents and dispersers, number of packs with two breeders in it).

Adaptation

Wolves live in packs and most of the processes coded in the model depend on the pack structure and the status of the individuals in the pack. The presence of zero, one of two breeders constrains the potential reproduction, pack dissolution, and replacement of breeding members. The total number of individuals in a pack constrains the pack dissolution, dispersal and adoption. The total number of established packs in the population also constrains some of the processes like the different probabilities of establishment (i.e., in pairs, by budding and alone) and one mortality process that have density dependent parameters.

Table A1
Parameters used in the wolf IBM. Probabilities and rates are estimates for a yearly time step.

Parameter	Sub-model in which the parameter is used (see Fig. A1)	Explanation	Value	Reference
Mean litter size	Reproduction	Number of pups that go out of the female den. Mean used for a Poisson distribution to generate the number of pups produced by a breeding pair.	6.1	Sidorovich et al. (2007)
Pup mortality	Mortality	Mortality probability for wolves in their first year of their life.	0.602	Smith et al. (2010)
Yearling mortality	Mortality	Mortality probability for non-dispersing yearlings.	0.18 (sd = 0.04)	Marucco et al. (2009)
Non density-dependent adult mortality	Mortality	Mortality probability for non-dispersing adults when the population is not at equilibrium density.	0.18 (sd = 0.04)	Marucco et al. (2009)
Density-dependent adult mortality	Mortality	Mortality probability for non-dispersing adults when the population is at equilibrium density. Mortality probability is calculated using the density-dependent survival φ as: logit(φ) = a + (b*((popDens-c)/d))), where popDens is the population density per 1000 km^2	a = -1.196 b = -0.505 c = 53.833 d = 17.984	Cubaynes et al. (2014)
Equilibrium density	Mortality; Establishment in pairs; Establishment by budding; Establishment alone	Maximum number of packs the environment within which the population is simulated can hold.	30	Defined by the user
Territory size	Mortality	Average territory size (in km^2) for wolves. Used to calculate the study area size with the equilibrium density to estimate wolf density through the model	104	Mancinelli et all. (2018)
Dispersing pup mortality	Mortality	Mortality probability for individuals that dispersed as pups and were not adopted by a pack during their dispersal year.	1	
Disperser mortality	Mortality	Mortality probability for dispersers (except individuals that dispersed as pups).	0.31	Blanco and Cortes (2007)
Dissolution probability for pack with 1 breeder	Pack dissolution	Probability of dissolution for small packs that have only 1 breeding individual left in the pack.	0.258	Brainerd et al. (2008)
Dissolution probability for pack with 0 breeders	Pack dissolution	Probability of dissolution for small packs that do not have any breeding individual left in the pack.	0.846	Brainerd et al. (2008)
Pack size threshold for dissolution	Pack dissolution	Pack size to differentiate large and small packs. Packs with fewer individuals than this threshold are considered small and can dissolve if only 1 or 0 breeding member remains.	Values tested: 3.1; 4.1; 5.1	
Relatedness threshold	Replacement of breeding females by subordinates; Establishment in pairs; Establishment by budding; Replacement of breeders by dispersers; Replacement of breeding males by subordinates	Relatedness value between 1st cousins. Two individuals must have their relatedness coefficient less than or equal to this threshold to be considered unrelated.	0.125	Caniglia et al. (2014)
Mean pack size	Dispersal; Adoption	Mean used for the Normal distribution to generate the sizes each pack can be. The size represents the maximum number of individuals each pack can hold.	4.405 (sd = 1.251)	Marucco and McIntire (2010)
Pup dispersal probability	Dispersal	Relative probability (compared to the other age categories) for a pup to leave the pack and become disperser.	0.25	Haight and Mech (1997)
Yearling dispersal probability	Dispersal	Relative probability (compared to the other age categories) for a yearling to leave the pack and become disperser.	0.5	Haight and Mech (1997)
Adult dispersal probability	Dispersal	Relative probability (compared to the other age categories) for an adult to leave the pack and become disperser.	0.9	Haight and Mech (1997)
Number of immigrants	Immigration/ Emigration	Number of immigrants arriving in the population each year. All values have the same probabilities to be chosen.	0, 1, or 2	Defined by the user
Proportion of emigrants	Immigration/ Emigration	Proportion of dispersing individuals that emigrate outside of the study area.	0.1	Defined by the user
Probability of adopting	Adoption	Probability for a pack that has less member than its maximum pack size to adopt a young disperser.	Values tested: 0.1; 0.5; 0.9	
Probability of budding	Establishment by budding	Probability of success for a disperser to establish a new pack by budding. This probability is multiplied by the density-dependent probability of establishment for the dispersers.	Values tested: 0.1; 0.5; 0.9	

Objectives

Wolves do not have an ultimate goal they need to fulfill over time. Individuals follow the behavioral rules of the different sub-models and respond to them according to their current characteristics and the current state of the packs.

Learning

There is no learning *per se* in the wolf IBM such as a learning of new skills (e.g., hunting prey taught by parents) but as individuals' age and status change, the possibilities for the individual change. For example, wolves of age 1, 2 and 3 years old can be adopted but not at an older age. Only mature wolves (of age 2 and older) can become breeders and establish a new territory; pups of 1 year old cannot. Only mature breeding wolves can reproduce; mature subordinates cannot.

Prediction

Individuals know the current state of the population and individuals' current characteristics but they cannot predict any future population or individual state nor any individuals' actions.

Sensing

Wolves in packs have knowledge of all individual characteristics for the other members in their pack. Packs that can adopt young wolves can sense the presence of young dispersers. Dispersing individuals have access to the packs and their structure as replacement of missing breeders by dispersers and pairing with a subordinate from a pack is possible for these individuals. There is no sensing of the environment as there is no interaction with it.

Interaction

Wolves are social animals and therefore multiple interactions shape the life cycle of this species. Reproduction requires two breeding individuals from the same pack to produce pups. Pack dissolution and dispersal represent a loss of interactions between individuals that were members of a pack and become dispersers due to various factors. In the replacement of missing breeders, there is a choice among the mature subordinates of the pack or among mature dispersers that may be constrained by the presence of the other breeding wolf. During establishment in pairs or by budding, a disperser interacts with another disperser or a subordinate in a pack to create a new territory.

Stochasticity

Stochasticity is included in almost all components of the model. The number of pups produced per breeding pair, the number of individual dying, the maximum number of individual allowed in a pack, the number of immigrants arriving in the population and the number of emigrants leaving are generated using probabilities. The following processes also occur probabilistically: pack dissolution based on the number of breeding members remaining in the pack, adoption, dispersal according to the individuals' age, and establishment by budding. Also, a density-dependent probability constrains the different types of establishment (i.e., in pairs, by budding and alone) as well as adult mortality when the population is at equilibrium density. The sex of the pups, the choice between unrelated individuals to replace missing breeders, the choice between young dispersers to be adopted, the choice between unrelated individuals to partner with a disperser to establish, and the choice of dispersing individuals that emigrate are done randomly. In the immigration process, as nothing is known about immigrating individuals, their sex and age (between a minimum and a maximum) is randomly assigned.

Collectives

Wolves belong to packs and their status of resident (i.e., inside a pack) or disperser (i.e., not belonging to a pack) affects almost all behavioral processes they follow. However, except for the pack dissolution, there is no process affecting the entire pack. As all individuals in the pack have different characteristics (i.e., age, sex, breeding status) they usually do not all respond in the same way.

Observation

The population is simulated for several years. Simulation outputs are available after each sub-model if needed or at the end of the whole series of sub-models at the end of the time step (i.e., at the end of the simulated year). The number of alive individuals with all their characteristics is available and many results can be extracted and derived from this population structure (e.g., the number of packs, the total abundance, the number of residents and dispersers, the number of breeders, the age distribution, etc.). We focused on outputs relevant for wolf conservation and management and defined six metrics. 1) At which year the population reached equilibrium density (i.e., in number of packs with a breeding pair). This output represents the speed of the population expansion and is a key element in areas that are being recolonized by the wolf. 2) The number of packs with two breeders. This metric is linked to the reproductive potential of the population and is of importance for management issues related to population growth. 3) The number of new packs formed in one year. This represents the pack turnover and the stability of the population that may affect hybridization and wolf-human conflicts. 4) The total number of individuals. 5) The proportion of residents and dispersers in the population. Population size is often required in management control and knowing the distribution of the resident/dispersing status of the individuals may help in understanding the population behavior. Finally, we looked at 6) the relatedness between the two breeders in each pack. Inbreeding avoidance plays a big part in the wolf life cycle, affecting the replacement of missing breeders and the creation of new packs. Often over looked because it is hard to simulate in non-individual-based models, this factor may indicate missing pieces in the models when not well represented.

Details

Initialization

To launch the IBM, an initial wolf population is needed. We built a fictive population of 10 packs and 5 dispersing wolves, in a fictive environment that can hold 30 packs total (i.e., equilibrium density, Table A1). We created 5 packs with 2 breeders (one male and one female, 5 years old each) and 2 pups (one male and one female, 1 year old each); 3 packs with 2 breeders (one male and one female, 5 years old each), 1 yearling (one male, 2 years old) and 1 pup (one female, 1 year old); 2 packs with 2 breeders (one male and one female, 5 years old each) and 1 adult (one female, 3 years old); and 5 dispersers (3 females, 2 males, 2 years old each). This simple population was created for convenience but other initial populations can be easily defined by users. Table A1 lists all parameters and their values used in the model. These parameters can also be easily modified by the user. However, they represent the best data currently available in the literature for gray wolves in Europe, or elsewhere if not available for Europe. For lesser-known processes which parameters are explored (i.e., pack dissolution, adoption, establishment by budding), all tested values are listed (Table A1).

Input data

There is no input data in the model. The environment is not represented and the initial population is not built using data.

Sub-models

reproduction: Every pack with both a breeding male and a breeding female reproduce (Marucco and McIntire 2010). The number of pups each pair has is drawn from a Poisson distribution (Chapron et al. 2016) with a mean of 6.1 (Sidorovich et al. 2007), representing the number of pups that emerge from the female den. Each pup receives a unique ID. The sex of each pup is randomly defined as male or female with a 1:1 ratio (Sidorovich et al. 2007, Marucco and McIntire 2010). Their age is set to 0 as all individuals (including these newborn pups) will go through the "aging" sub-model next. Pups are considered residents, with the pack ID of their parents. They are not breeders. Their mother and father IDs are recorded and they obtain a cohort ID equal to the current simulated year (i.e., all pups born the same year have the same cohort ID).

aging: All individuals age 1 year. Pups of the year are now 1 year old, yearlings are 2, and 3-year olds and older are adults. Individuals are considered mature at 2 years old (i.e., yearlings and adults).

mortality: There are 7 different mortality rates that take into account age, residence status and the total number of packs relative to equilibrium density. Mortality is applied individually to each wolf using a Bernoulli distribution which probability is sampled from a Normal distribution at each time step. Pups have a probability of 0.602 of dying (Smith et al. 2010). The mortality probability for non-dispersing yearlings is equal to 0.18 (sd = 0.04, Marucco et al. 2009). There are two types of mortality for non-dispersing adults that depend on the number of established packs in the population. If the number of established packs is below the number of packs at equilibrium density of the area, mortality is fixed and equal to that of the yearlings (i.e., 0.18 with sd = 0.04 (Marucco et al. 2009)). However, if the number of established packs is equal to the equilibrium density of the area, mortality is density-dependent. We used the equation linking wolf survival φ with wolf density from Cubaynes et al. (2014) to estimate the density-dependent mortality for non-dispersing adults: logit(φ) = 1.196 + (-0.505 * popDensStd), where popDensStd is the wolf density per 1000 km^2 standardized with Cubaynes' mean and standard deviation values (mean = 53.833, sd = 17.984). Wolf density is calculated as the total number of wolves, without considering the pups, divided by the area where the population is, estimated as the equilibrium density defined by the user multiplied by the wolf average territory size (104 km^2, Mancinelli et al. 2018). Two mortality rates concern dispersing individuals. No pups can be dispersers and dispersing yearlings are individuals that dispersed the previous year (when they were pups due to a dissolution of their pack) but could not find a pack to adopt them during that year (otherwise they would be residents). We assumed these individuals are too young to survive by themselves and we defined a mortality probability equal to 1 to dispersing yearlings. All other dispersing wolves (i.e., adults) have a mortality probability equal to 0.31 (Blanco and Cortes 2007). We did not model senescence or any increase of the mortality probability with age. To represent a realistic age distribution in the population, the limit for wolves was the end of their 15th year of simulation (Marucco and McIntire, 2010) and all individuals reaching 16 years old die.

packDissolution: Following the mortality event, packs whose social structure has been impacted by the loss of breeders may dissolve (Brainerd et al. 2008). Small packs with 1 breeding individual remaining will dissolve with a probability of 0.258 (Brainerd et al. 2008), and small packs with no breeder left dissolve with a probability of 0.846 (Brainerd et al. 2008). The pack size threshold to differentiate small and large packs was explored using the values 3.1, 4.1 and 5.1. In the specific case where both breeders died and only pups remain, the pack always dissolves as we assumed pups alone are unlikely to maintain a territory and so they disperse. When a pack dissolves, all former members of the pack become dispersers, they do not belong to a pack anymore and former breeding individuals lose their status.

replaceBreedingFemBySub: When a breeding female dies, she is most likely replaced by one of the female subordinates in her pack (most likely one of her daughters) (Caniglia et al. 2014; Jedrzejewski et al. 2005). When a pack is missing its breeding female, one of the mature females from the pack is randomly chosen to become breeder. Once the new breeding female is chosen we look at the relatedness between her and the current breeding male, if there is any. If there is a breeding male in the pack and he is closely related to the chosen female, he may be replaced (in sub-models *replaceBreederByDisp* and *replaceBreedingMalBySub*) by a disperser or a less related subordinate from the pack who will usurp the established breeding position (Mech and Boitani, 2003). The relatedness threshold chosen is the one of the first cousin (r = 0.125); a mating pair of breeding wolves can be no more closely related than cousins (e.g., no mating between siblings or parents and children) (Caniglia et al. 2014). This relatedness threshold is the same for all sub-models.

dispersal: When a pack has too many wolves, some are chased away and become dispersers. A maximum number of individuals is generated for each pack at each time step using a Normal distribution with a mean of 4.405 (sd = 1.251, Marucco and McIntire 2010). If the pack has more wolves than its maximum threshold, some individuals will leave the pack until the number of wolves in the pack is equal to its threshold. Breeding individuals cannot disperse. All the other wolves can disperse but with different relative probabilities based on their age. Pups may disperse with a

relative probability of 0.25, yearlings may disperse with a relative probability of 0.5, and adults may disperse with a relative probability of 0.9 (Haight and Mech 1997). Wolves leaving the pack become dispersers and do not belong to the pack anymore.

immigration: Some wolves outside of the simulated population can arrive and interact with the other wolves. A user-determined number of immigrants will integrate with the population. The sex of the immigrants is randomly assigned (i.e., male or female with a 1:1 ratio). Their age is simulated using a truncated Poisson distribution of mean equal to 2 (with boundaries between 1 and 15) as yearlings are the most likely to disperse. Immigrants are dispersers, they do not belong to any pack yet and they are not breeders. As they were born outside the simulated population, they do not hold information about their mother, father or cohort IDs. Immigrant wolves will react the same way (i.e., follow the same sub-model rules) as the native wolves.

emigration: A proportion of the currently dispersing individuals, randomly chosen, leaves the simulated population via long-distance dispersal. These individuals will not come back and their disappearance is similar to simulating their death.

adoption: Packs which are not full (i.e., their number of individuals is below their maximum threshold) can adopt individuals. The probability with which these packs will adopt was explored using the values 0.1, 0.5, and 0.9. These packs can adopt individuals until they reach their maximum number of pack members. Only dispersers of 1, 2 and 3 years of age can be adopted by these packs. The order in which packs adopt dispersing individuals is random. Among potential adoptees, males are selected first. Then, if there are no more males and packs are still able to adopt, females are chosen. The choice among the males or among the females is random. Once young dispersers have been adopted, they become residents and belong to the pack that adopted them.

replaceBreederByDisp: Missing breeders in packs can be replaced by dispersers. First, we look at the packs missing breeding females. Mature female dispersers can become breeding females. If there is already a breeding male in the pack, we exclude the dispersing females that are closely related to the breeding male from the potential successors. Then, a female is randomly chosen among the unrelated ones to integrate into the pack. All selected females become residents and breeders of their assigned pack, and belong to the pack they joined. The order in which packs fill breeding female positions is random. Next, the same process is used to replace missing male breeders with mature male dispersers. If there are packs where the missing breeding female was replaced by a subordinate (in *replaceBreedingFemBySub*) during the time step and the current breeding male was too related to her, an unrelated, mature male disperser may usurp the established male breeder (Mech and Boitani, 2003). The breeding males replaced by dispersers are dismissed from their position and become subordinates in their own pack.

establishPairs: A male disperser and a female disperser can establish a new pack together if they are mature and not closely related. In addition, this is only possible if the number of existing packs is not already equal to equilibrium density. If the area is not already full, there is a density-dependent probability for dispersers to establish in pairs defined by a Bernoulli distribution with a probability equal to the number of packs that can be created until reaching equilibrium density divided by the equilibrium density. The more packs there are, the less likely it is that two dispersers establish themselves in pairs. Once a male and a female disperser have established a new pack, they both become breeders and residents, and obtain the same, new and unique pack ID. The order for the choice of males and females among the available mature dispersers is random.

establishBudding: Budding is when a disperser and a mature subordinate wolf from an existing pack establish a new pack together. Like establishment in pairs, budding is possible only if the number of packs has not reached equilibrium density. The probability for a disperser to bud is the density-dependent probability for establishment in pairs multiplied by a probability of budding. We explored this last probability and tested values equal to 0.1, 0.5 and 0.9. Only mature dispersers can bud, and only with a non-breeding, mature resident of the opposite sex that is not closely related. Once a disperser and a subordinate wolf bud, they both become breeders and residents, and obtain the same, new and unique pack ID. The order for the choice of males and females among the available mature dispersers and subordinates in packs is random.

establishAlone: If the area is not at equilibrium density, remaining mature dispersers that could not establish themselves in pairs or by budding can establish themselves alone. The probability of this is also density-dependent, and is the same as the probability of the establishment in pairs. Once they create their own pack, wolves become breeders and residents, and obtain a new and unique pack ID.

replaceBreedingMalBySub: When a breeding male is missing, one of the mature, male subordinates in the pack can take over. If there are several subordinates that are eligible to become successors, the male least related to the current breeding female is chosen. If there are several subordinate males that are the least related, or if there is no breeding female, one is selected randomly. If the breeding female is too related to the newly chosen breeding male, the mature, female subordinate who is least related to the new breeding male can usurp the current breeding female and the current breeding female is dismissed (i.e., becomes subordinate). If there are several mature female subordinates that are the least related, one is selected randomly. In the particular case where there was a missing breeding female who was replaced by a subordinate (in *replaceBreedingFemBySub*) during the time step and she was too related to the current breeding male, one of the less related male subordinates can take over the male breeding position. All of these rules mimic the fact that wolves change partners to avoid inbreeding, except when there is no other choice (Mech and Boitani, 2003). Once new breeding individuals are chosen, they will be able to mate the next year.

Appendix B

All 81 model scenarios tested by combining the 3 parameterizations of the pack dissolution process (Table 2, main text), with the 3 parameterizations of the adoption process (Table 2, main text), with the 3 parameterizations of the establishment by budding process (Table 2, main text), and with the 3 model versions for the breeder replacement process (Fig. 1, main text).

Model scenario	Pack dissolution threshold	Adoption probability	Budding probability	Model version
S1	3.1	0.1	0.1	M1
S2	4.1	0.1	0.1	M1
S3	5.1	0.1	0.1	M1
S4	3.1	0.5	0.1	M1
S5	4.1	0.5	0.1	M1
S6	5.1	0.5	0.1	M1
S7	3.1	0.9	0.1	M1
S8	4.1	0.9	0.1	M1
S9	5.1	0.9	0.1	M1
S10	3.1	0.1	0.5	M1

S11	4.1	0.1	0.5	M1
S12	5.1	0.1	0.5	M1
S13	3.1	0.5	0.5	M1
S14	4.1	0.5	0.5	M1
S15	5.1	0.5	0.5	M1
S16	3.1	0.9	0.5	M1
S17	4.1	0.9	0.5	M1
S18	5.1	0.9	0.5	M1
S19	3.1	0.1	0.9	M1
S20	4.1	0.1	0.9	M1
S21	5.1	0.1	0.9	M1
S22	3.1	0.5	0.9	M1
S23	4.1	0.5	0.9	M1
S24	5.1	0.5	0.9	M1
S25	3.1	0.9	0.9	M1
S26	4.1	0.9	0.9	M1
S27	5.1	0.9	0.9	M1
S28	3.1	0.1	0.1	M2
S29	4.1	0.1	0.1	M2
S30	5.1	0.1	0.1	M2
S31	3.1	0.5	0.1	M2
S32	4.1	0.5	0.1	M2
S33	5.1	0.5	0.1	M2
S34	3.1	0.9	0.1	M2
S35	4.1	0.9	0.1	M2
S36	5.1	0.9	0.1	M2
S37	3.1	0.1	0.5	M2
S38	4.1	0.1	0.5	M2
S39	5.1	0.1	0.5	M2
S40	3.1	0.5	0.5	M2
S41	4.1	0.5	0.5	M2
S42	5.1	0.5	0.5	M2
S43	3.1	0.9	0.5	M2
S44	4.1	0.9	0.5	M2
S45	5.1	0.9	0.5	M2
S46	3.1	0.1	0.9	M2
S47	4.1	0.1	0.9	M2
S48	5.1	0.1	0.9	M2
S49	3.1	0.5	0.9	M2
S50	4.1	0.5	0.9	M2
S51	5.1	0.5	0.9	M2
S52	3.1	0.9	0.9	M2
S53	4.1	0.9	0.9	M2
S54	5.1	0.9	0.9	M2
S55	3.1	0.1	0.1	M3
S56	4.1	0.1	0.1	M3
S57	5.1	0.1	0.1	M3
S58	3.1	0.5	0.1	M3
S59	4.1	0.5	0.1	M3
S60	5.1	0.5	0.1	M3
S61	3.1	0.9	0.1	M3
S62	4.1	0.9	0.1	M3
S63	5.1	0.9	0.1	M3
S64	3.1	0.1	0.5	M3
S65	4.1	0.1	0.5	M3
S66	5.1	0.1	0.5	M3
S67	3.1	0.5	0.5	M3
S68	4.1	0.5	0.5	M3
S69	5.1	0.5	0.5	M3
S70	3.1	0.9	0.5	M3
S71	4.1	0.9	0.5	M3
S72	5.1	0.9	0.5	M3
S73	3.1	0.1	0.9	M3
S74	4.1	0.1	0.9	M3
S75	5.1	0.1	0.9	M3
S76	3.1	0.5	0.9	M3
S77	4.1	0.5	0.9	M3
S78	5.1	0.5	0.9	M3
S79	3.1	0.9	0.9	M3
S80	4.1	0.9	0.9	M3
S81	5.1	0.9	0.9	M3

Appendix C

All model outputs from the 81 model scenarios tested (see Appendix B). Output shown over time (i.e., line figures) present the mean values and their 95% confidence intervals, per year, from the 200 replicates for each model scenario. Boxplots present model outputs extracted at the end of the last simulated year from all 200 replicates for each model scenario tested. Lines and boxplots are color-coded (and ranked for boxplots only) according to the different values or model versions tested to explore the sub-models simulating lesser-known wolf dynamics processes: a) pack dissolution (see Table 2, main text), b) adoption (see Table 2, main text), c) establishment by budding (see Table 2, main text), and d) breeder replacement (see Fig. 1, main text).

Figs. C1, C2, C3, C4, C5 and C6

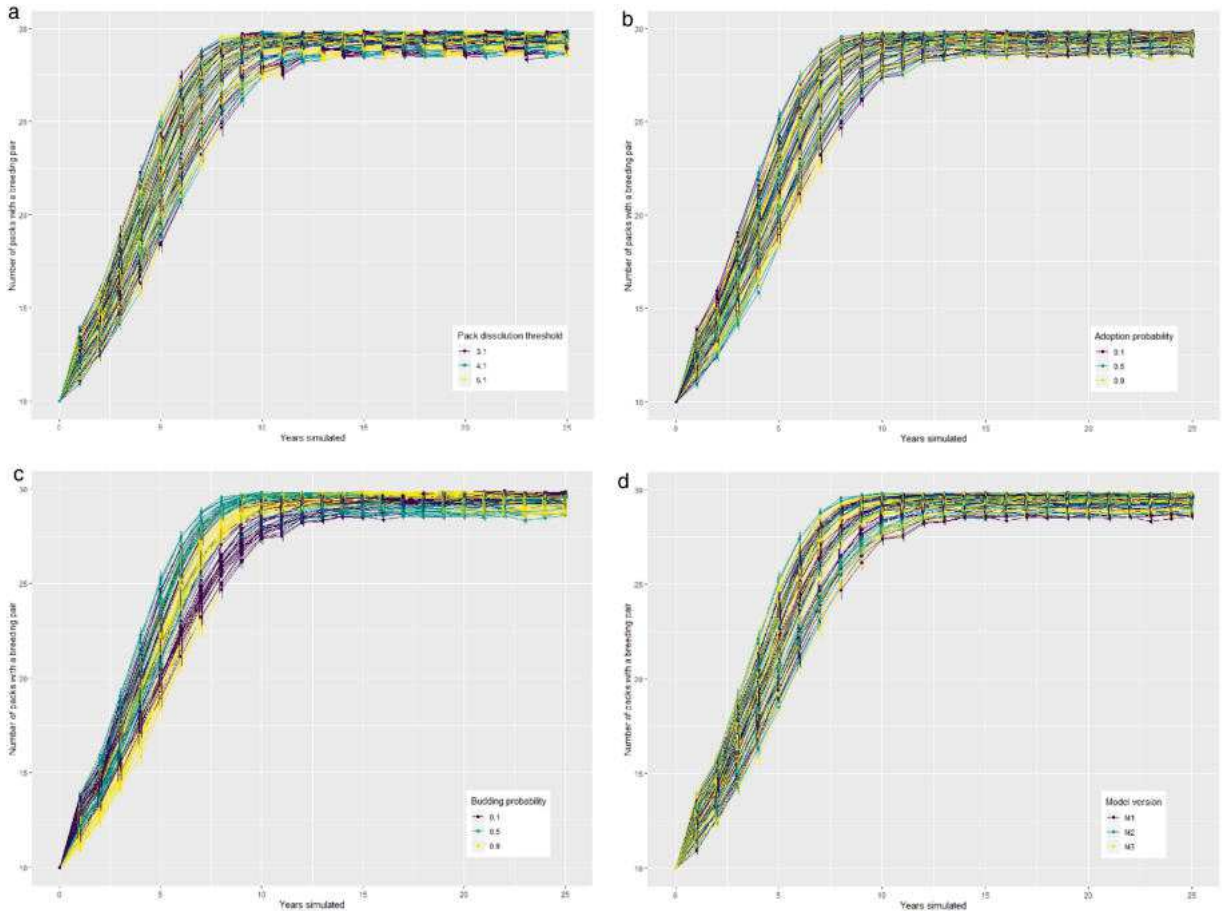

Fig. C1. Number of packs with a breeding pair over the simulated years for each model scenario.

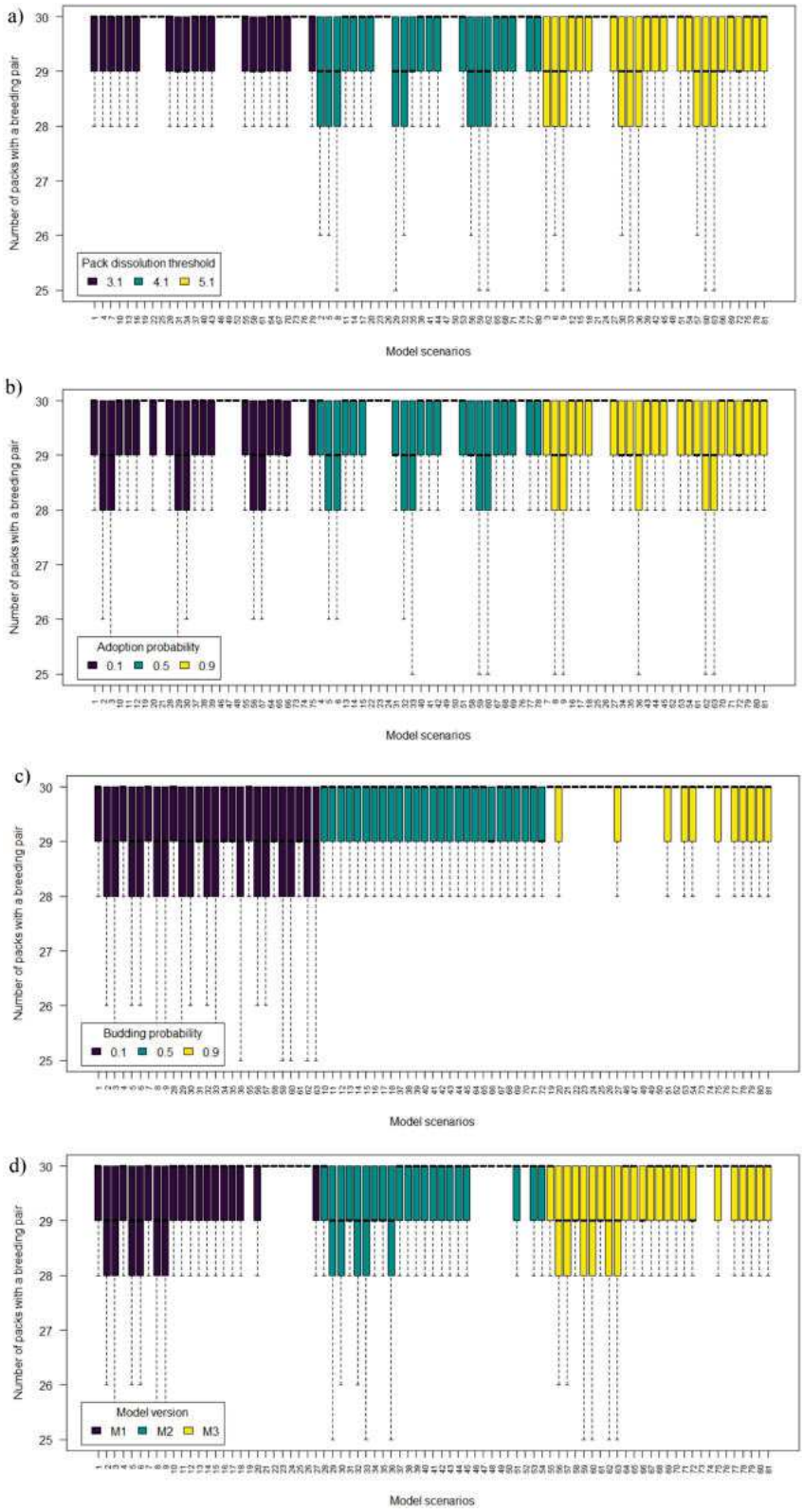

Fig. C2. Number of packs with a breeding pair at the end of last simulated year for each model scenario (Appendix B).

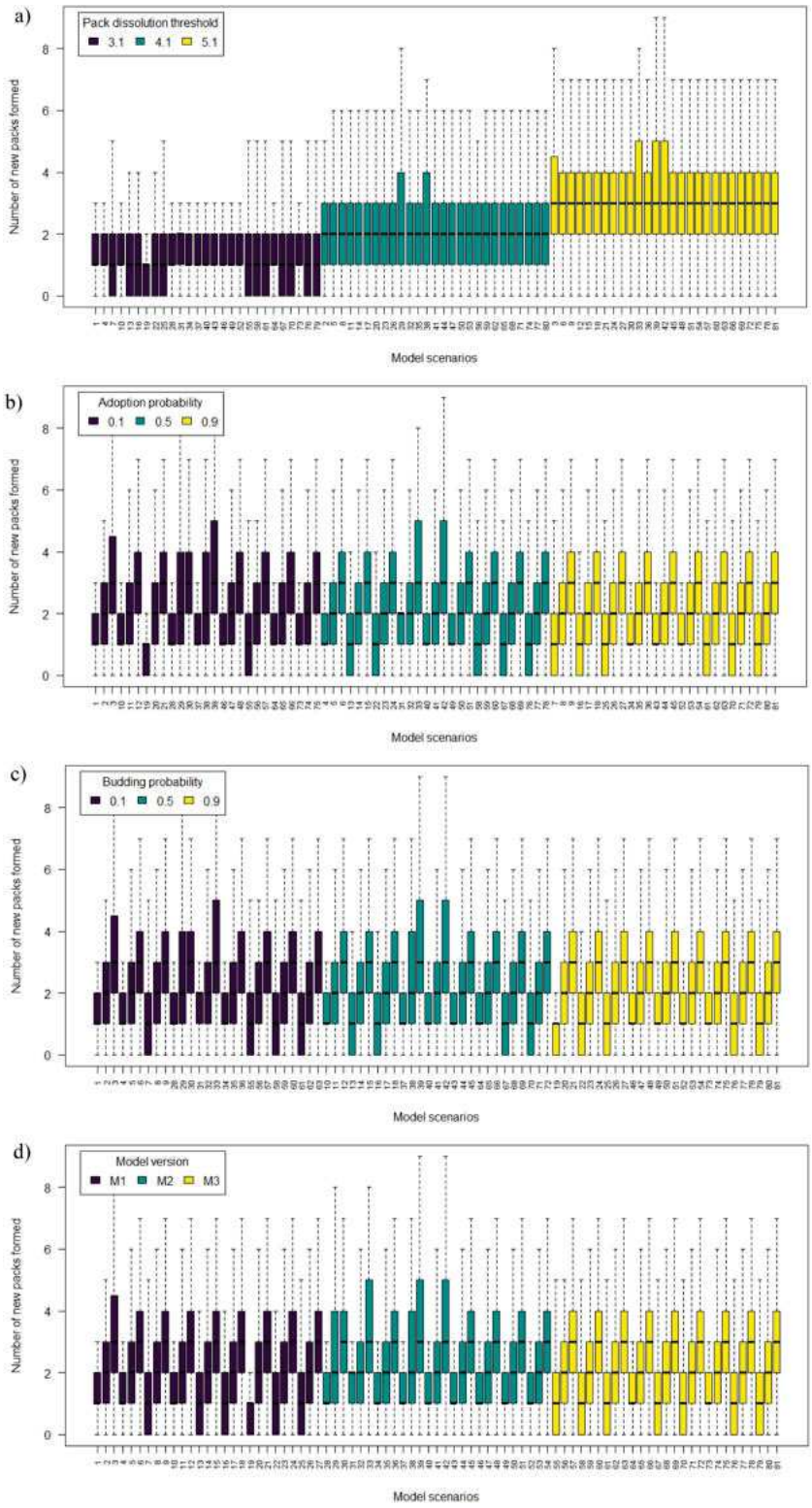

Fig. C3. Number of new packs created during the last simulated year for each model scenario (Appendix B).

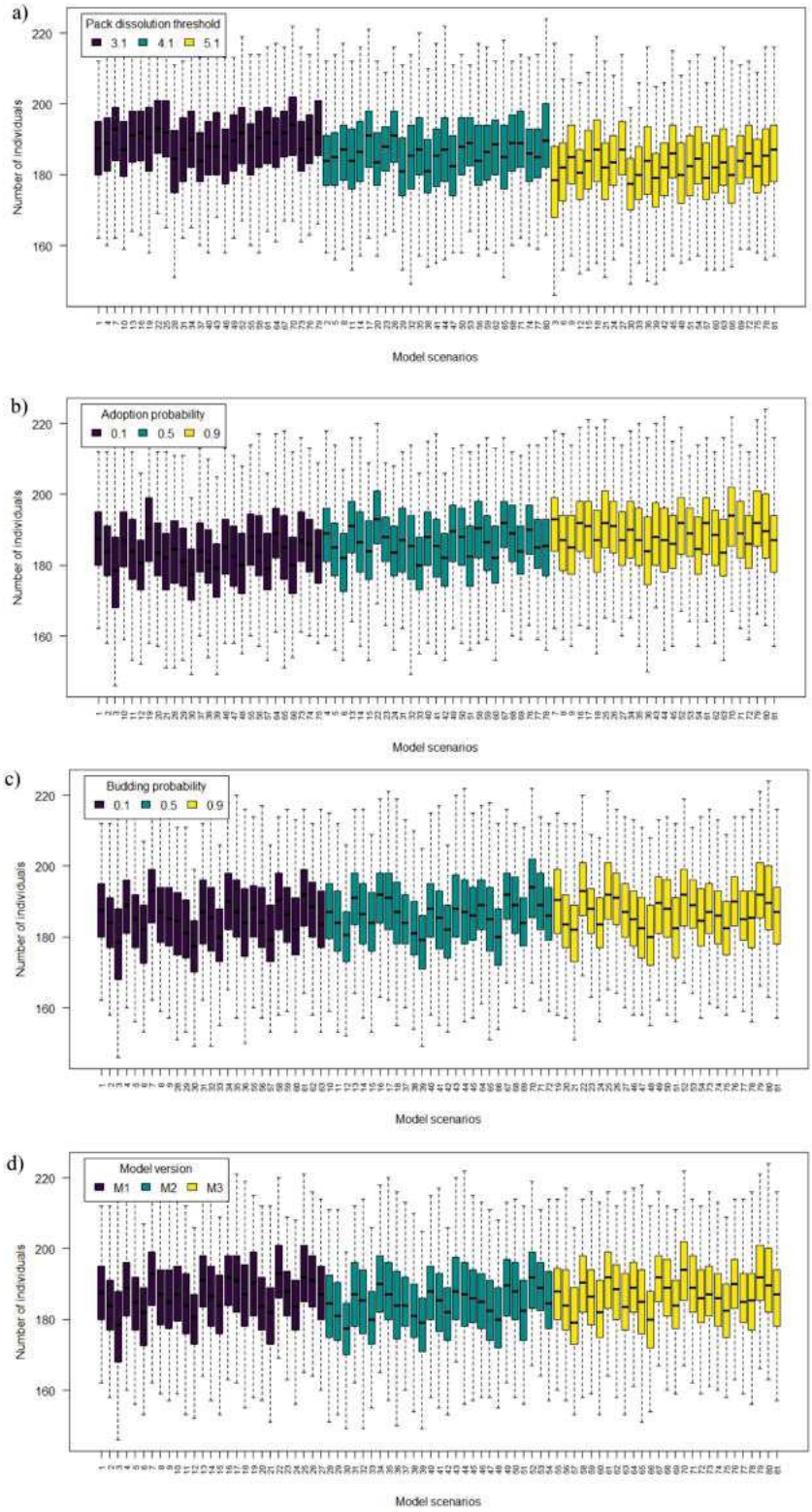

Fig. C4. Total number of individuals in the population at the end of last simulated year for each model scenario (Appendix B).

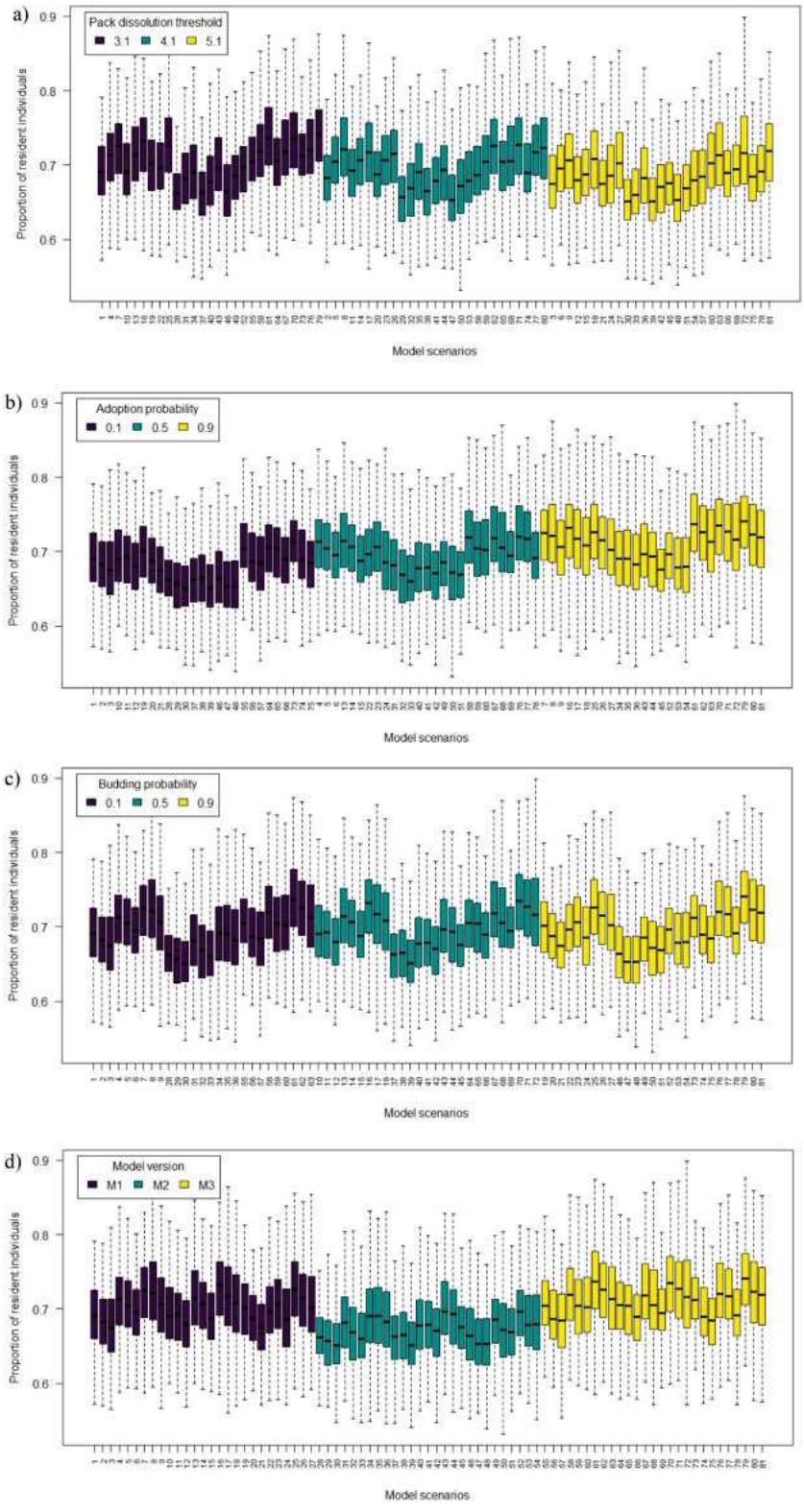

Fig. C5. Proportion of resident individuals in the population at the end of last simulated year for each model scenario (Appendix B).

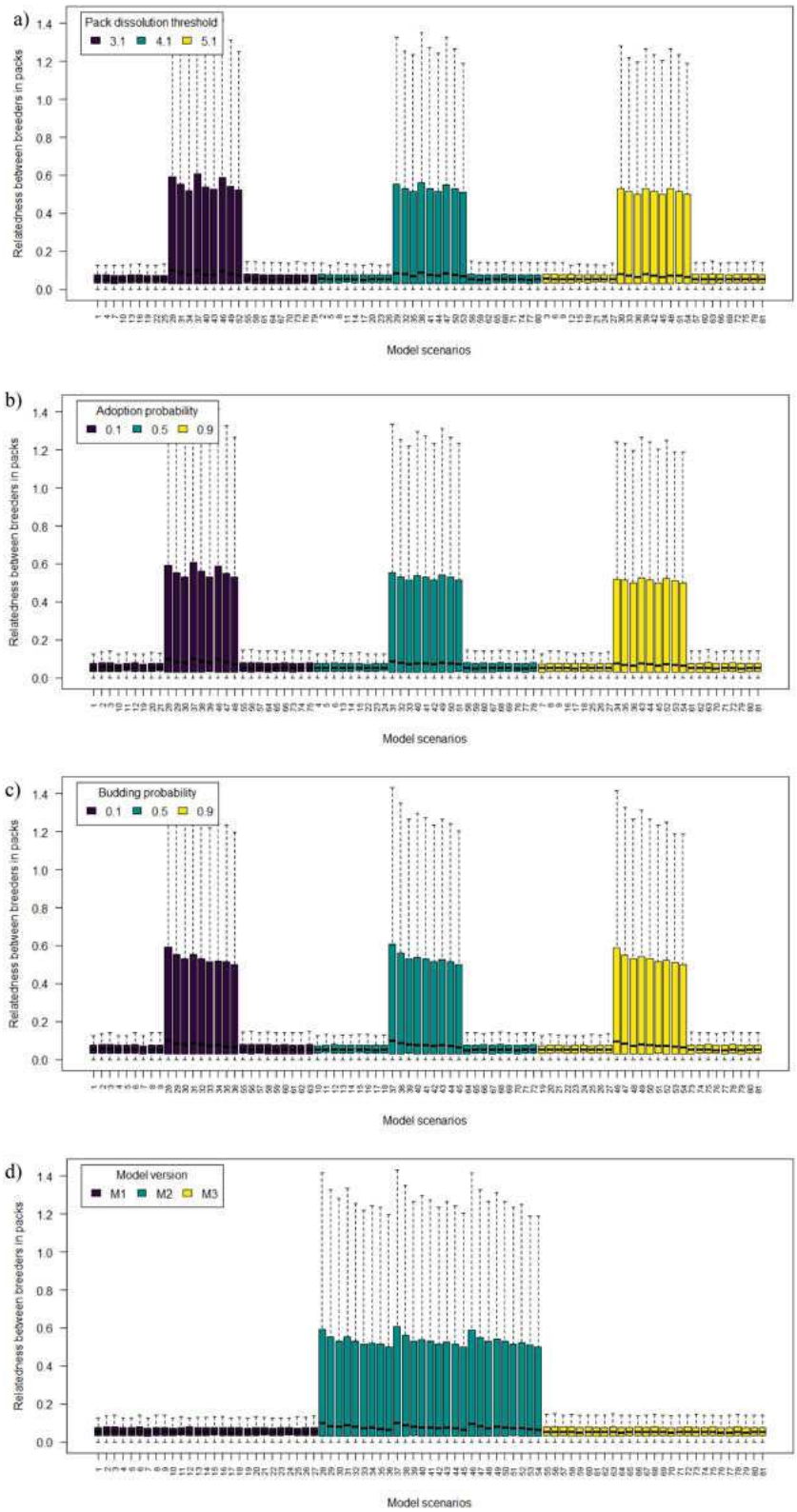

Fig. C6. Relatedness value between the male and female in breeding pairs at the end of last simulated year for each model scenario (Appendix B).

Appendix D

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2020.109209.

Complete results of the sensitivity analysis. The first line of the table is the name of the simulation run: SA0 for the reference model and the runs SA1 to SA36 are the runs similar to SA0 where one parameter of the model was modified, one at a time, with its value either decreased or increased by 5%. SA0 is the model version M1 (Fig. 1, main text), with the value 4.1, 0.5, and 0.5 for the parameters of sub-models pack dissolution, adoption and establishment by budding respectively (model scenario S14 from Appendix B), and the parameter values from the up-to-date literature for the other sub-models (Table 1, main text). The second line of the table informs which parameter was modified in the sensitivity analysis run and the following line gives the value used for this parameter. Then, the six following line are the six model outputs: the year at which populations reached equilibrium density, the number of packs with a breeding pair, the number of new packs created, the number of individuals, the proportion of resident individuals and the relatedness between the individuals in breeding pairs. The result values are the mean values over the 200 simulation replicates for each run. The column "SA0 [- 20%; + 20%]" presents the results for the run with reference model with the range – 20% and + 20% of the result values. Then, table cells are the mean values of the model outputs obtained with the runs SA1 to SA36. Dark orange cells are model results outside of the reference range of M0 results [- 20%; + 20%], light orange cells are the lowest and highest values for the model outputs.

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The depredation behaviour | B

This appendix completes Chapter 2 (The depredation behaviour) on page 57.

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B.1 Required minimum number of replicates

The IBM of Chapter 1 and Chapter 2 involved stochastic processes. According to [296], *'a stochastic process is one in which the state of the system cannot be precisely predicted given its current state, even with a full knowledge of all the factors affecting that process.'*. For example, the number of pups produced by a breeding pair was modelled as a Poisson distribution of mean 6.1 in the IBM [191]. This meant that we could predict that the number of pups would approximate 6 most of the time, but it could not be known for sure in advance. It was still possible to have a number of pups of 2 or 12 for a breeding pair during a cycle even if it was less likely. This is why we could not rely on only just one simulation of our IBM. Indeed, imagine that the breeding pairs of our model all produced very large litters of at least 10 pups in a simulation of 150 time steps: it is extremely unlikely, but still possible. In this case, this would not reflect the general tendency that we expected from our model, even when considering variations around the mean as possible. If we relied only on this simulation, this could lead us to wrong conclusions. Besides, a lot more processes of the IBM were stochastic, not only the number of pups.

[296]: Possingham et al. (2013), 'Population Viability Analysis'

[191]: Bauduin et al. (2020), 'An Individual-Based Model to Explore the Impacts of Lesser-Known Social Dynamics on Wolf Populations'

We therefore needed to make sure to get rid of extreme simulations. The only way to do so were to multiply the number of simulations. We called two simulations of the same model '*replicates*'. Because each scenario we modelled for both Chapter 1 and Chapter 2 had to be considered as a model, different from the other scenarios, replicates had to be done for each scenario.

In Chapter 1, we used 200 replicates, but for a period six times shorter than for the models from Chapter 2. Therefore, we could use 200 replicates or less for the models of Chapter 2. To decide, we computed for randomly-selected 25 scenarios the annual mean of three parameters (the number of individuals, of packs and the DI population sum) averaged over 50, 100, 150 and 200 replicates over 150 time steps. Results are provided below.

To read the results, you need to focus on the parameter's variations. The variations has to be looked for each scenario at a time and not compared to the variations of other scenarios. In short, you should look at one line at a time, for each panel of each figure (*e.g.* the panel 50 replicates for parameter 'population size'). Then, you can switch to the next panel (*e.g.* the panel 100 replicates for parameter 'population size'), and see how the variations for those same lines evolved compared to the previous panel.

For the three parameters, we noticed that the variations across time steps were maximal for 50 replicates, and decreased with the number of replicates, as expected. In short, the lines were more '*waving*' at 50 replicates than at 200 replicates, and their 95% confidence intervals were getting smaller. This meant that for 50 replicates, the mean of 50 replicates for a given parameter and a given scenario was not as stabilised as the mean of 200 replicates. In short, there was not enough replicates to smooth the means at 50 replicates, meaning extreme simulations had still a too important weight on the mean, therefore exposing us to wrong conclusions.

We noticed that the stabilisation of means were effective from 150 replicates, and that the differences at 200 replicates were negligible. To have the best compromise between computational times (requiring the lowest possible number of replicates) and result quality (requiring a large number of replicates), **we chose to replicate 150 times each scenario of our IBM model from Chapter 2**.

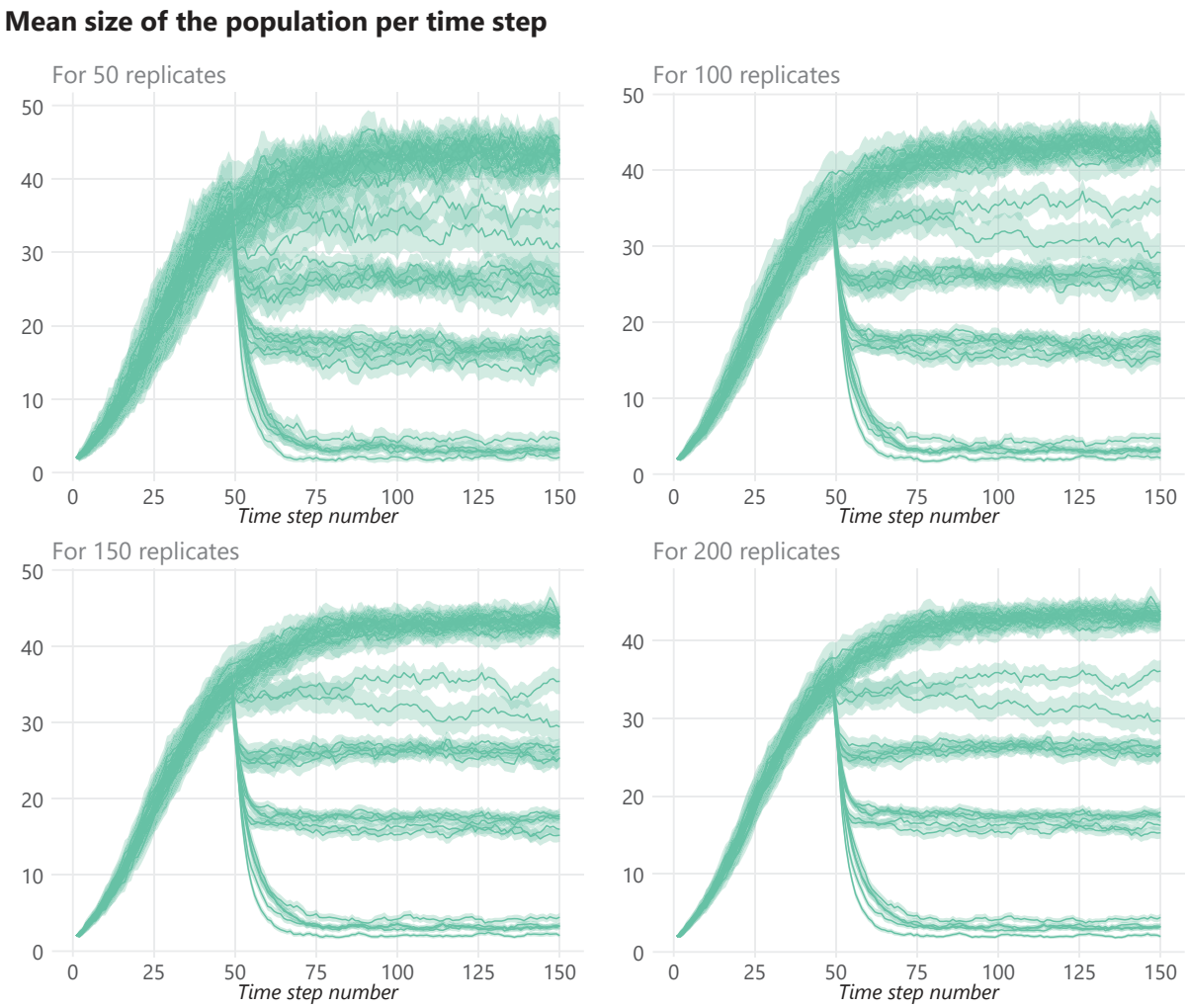

Figure B.1: Means of population size per time step and their 95% Confidence Intervals for 25 randomly-selected scenarios from the IBM in Chapter 2. The scenarios could involve any type of hypotheses regarding the depredation or culling components, and any type of viability threshold (0, 0.5 or 0.8). Each line represents the mean of population size for one scenario. A time step represents one year in the IBM. Credits: O. Grente

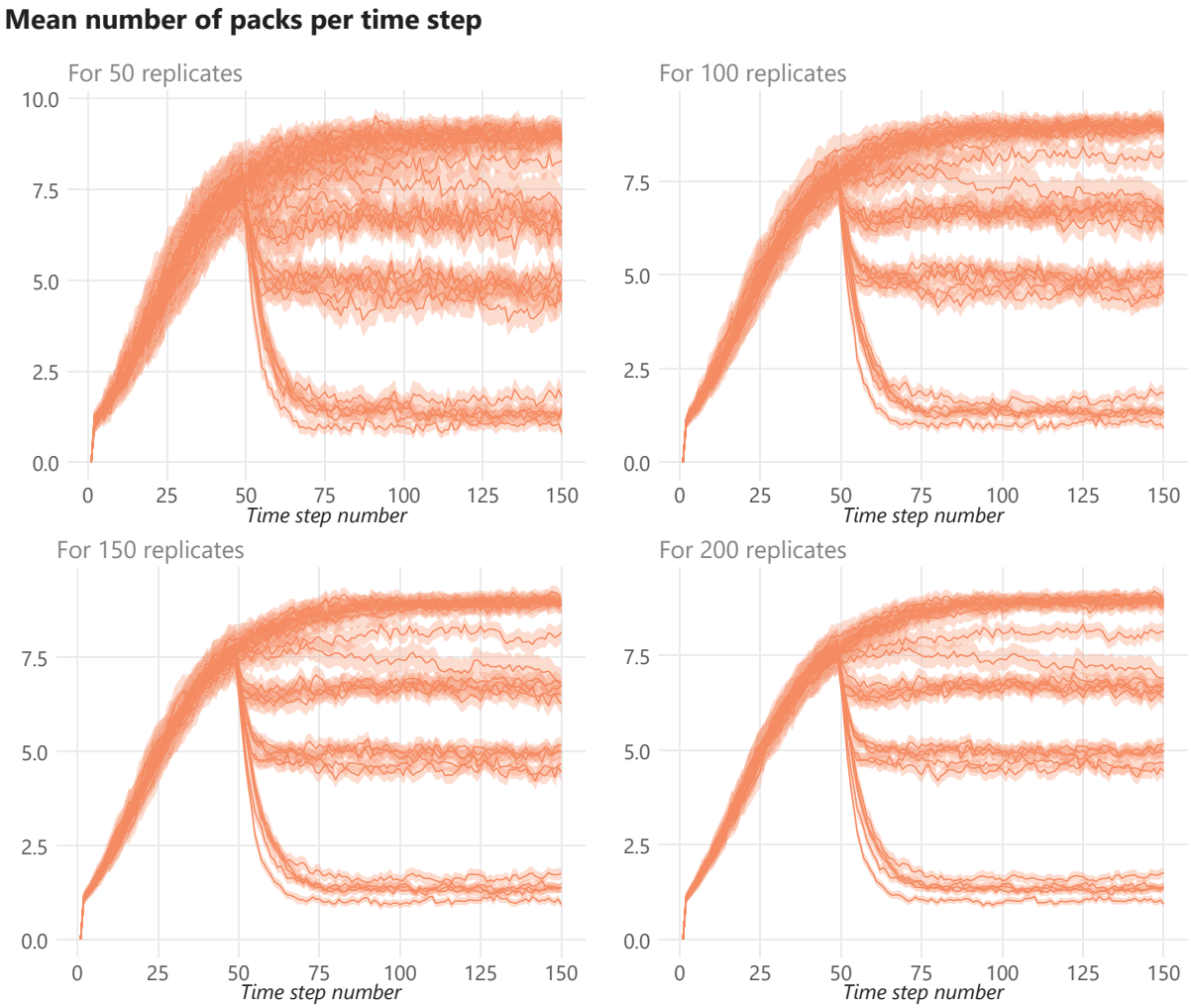

Figure B.2: Means of pack number per time step and their 95% Confidence Intervals for 25 randomly-selected scenarios from the IBM in Chapter 2. The scenarios could involve any type of hypotheses regarding the depredation or culling components, and any type of viability threshold (0, 0.5 or 0.8). Each line represents the mean of pack number for one scenario. A time step represents one year in the IBM. Credits: O. Grente

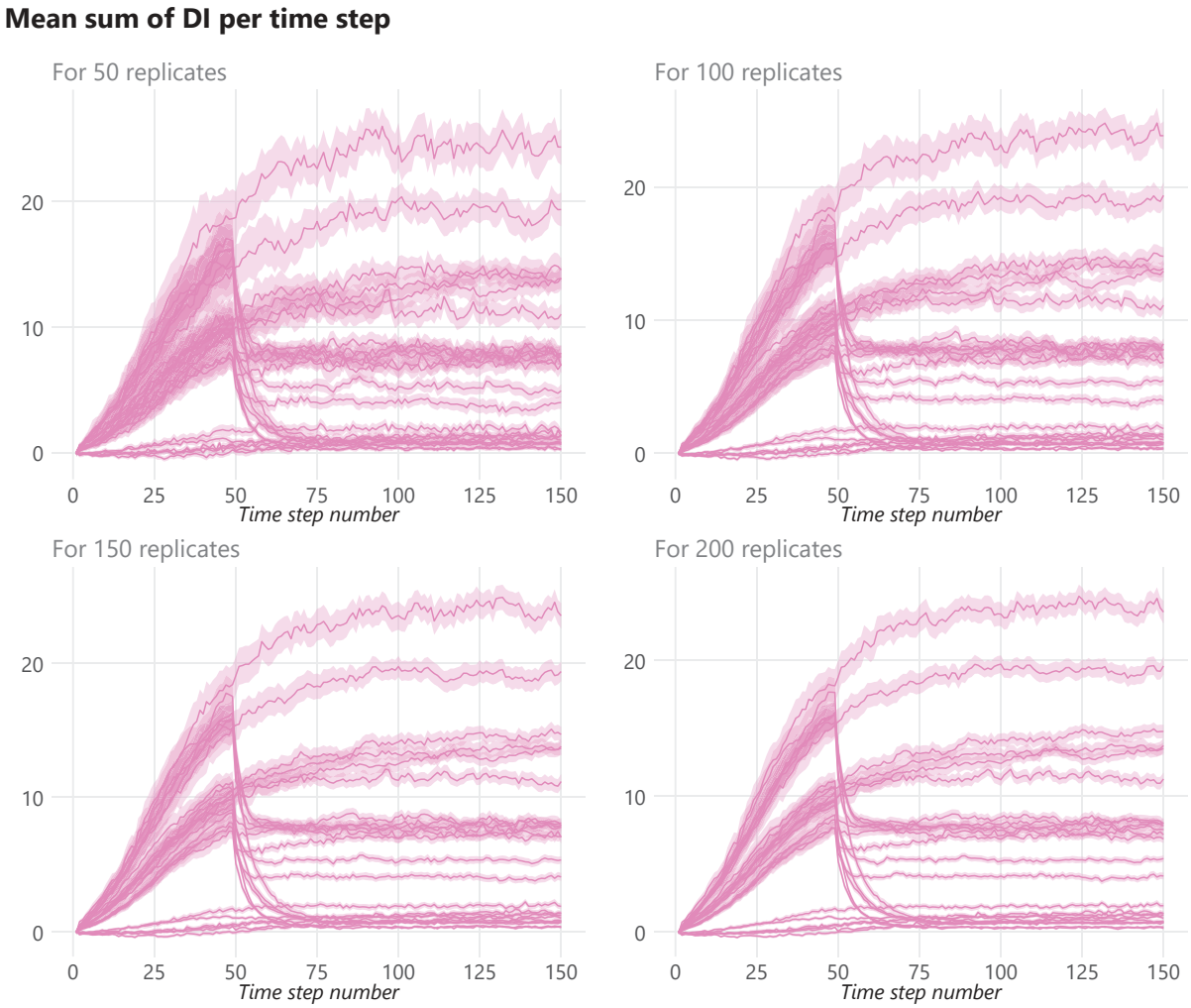

Figure B.3: Means of DI sum of the population per time step and their 95% Confidence Intervals for 25 randomly-selected scenarios from the IBM in Chapter 2. The scenarios could involve any type of hypotheses regarding the depredation or culling components, and any type of viability threshold (0, 0.5 or 0.8). Each line represents the mean of DI sum of the population for one scenario. A time step represents one year in the IBM. Credits: O. Grente

B.2 The effects of culling

This completes the results from section 2.4 (The effects of culling) on page 104.

Context 0: livestock as vulnerable as wild preys

This completes the results when the hunting efficiency hypothesis is considered as H_0 (*Context 0: livestock as vulnerable as wild preys*).

In this context, livestock are considered as vulnerable as wild preys. If there is no large difference between prey vulnerabilities, then the differences of hunting efficiency amongst wolves are therefore not expected to influence the depredation pattern. In short, whether the wolf is in a large pack or not, whether it is an adult or a subadult, this does not influence its depredation risk in this context.

Configurations for the territory knowledge and learning hypotheses

We present here only the results for which the **viability threshold was 50%**.

The explored configuration are H_0 for both the territory knowledge and learning hypotheses (Figure B.4a), H_1 for the territory knowledge hypothesis and H_0 for the learning hypothesis (Figure B.4b) and H_0 for the territory knowledge hypothesis and H_1 for the learning hypothesis (Figure B.4c).

The scenarios corresponding to these configurations are presented in Table B.1.

Table B.1: The three culling scenarios (last line) analysed under the context of H_0 for hunting efficiency and three different configurations for both territory knowledge and learning, respectively used in Figure B.4a, Figure B.4b and Figure B.4c.

(a) Scenarios in Figure B.4a

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE	✓		
PHE	✓		
IL	✓		
PL	✓		
Culling	✓	✓	✓

(b) Scenarios in Figure B.4b

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE	✓		
PHE	✓		
IL	✓		
PL	✓		
Culling	✓	✓	✓

(c) Scenarios in Figure B.4c

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE	✓		
PHE	✓		
IL		✓	
PL		✓	
Culling	✓	✓	✓

The viability thresholds

Up to now, only the viability threshold of 50% has been used under the context 0 hunting efficiency (H_0). Let's consider now the two other viability thresholds for this context, 0% and 80%. We keep the same scenarios as the ones shown in the main text (Table 2.9): the three culling scenarios with H_0 for hunting efficiency and H_1 for both territory knowledge and learning (at both the individual and pack levels).

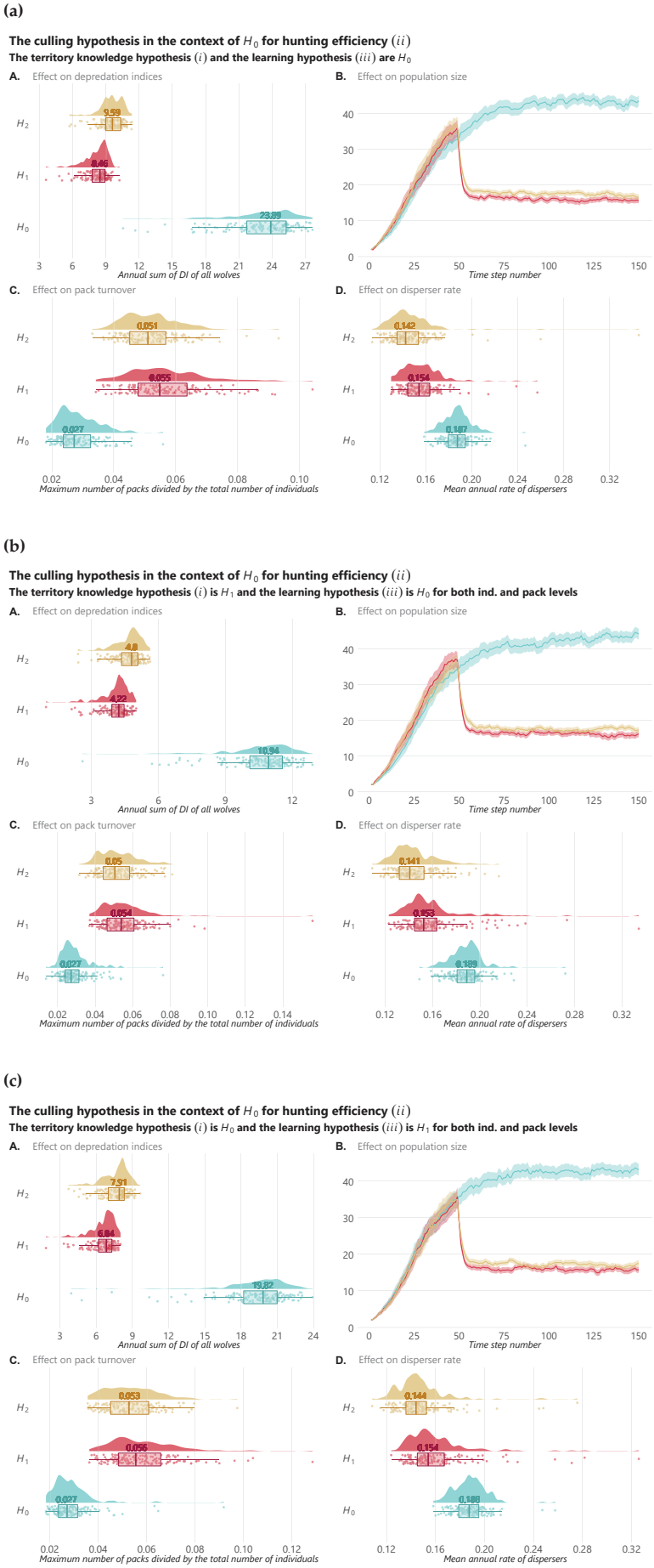

Figure B.4: Dashboard of the effect of the three different culling managements under the context of H_0 for hunting efficiency, and three additional configurations for territory knowledge and learning. The blue results refer to an absence of culling management, the red results refer to the selective culling management H_1 and the yellow results refer to the random culling management H_2. The culling managements are explained in *The culling scenarios*. Panels A. and D. reflect the results over the time steps period 50-150. For panel B., the ribbon represents the 95% Confidence Interval of the mean. The visualisation of each parameter is explained in greater detail in Table 2.8. Credits: O. Grente

Under a viability threshold at 0%, this meant that the culling managements were triggered at every time step from the 50th time step, regardless of population size. Under a viability threshold at 80%, this meant that the culling managements could only be triggered if the population exceeded $0.8 \times 50 = 40$ individuals after the Reproduction and Mortality components at the beginning of each time step, from the 50th time step.

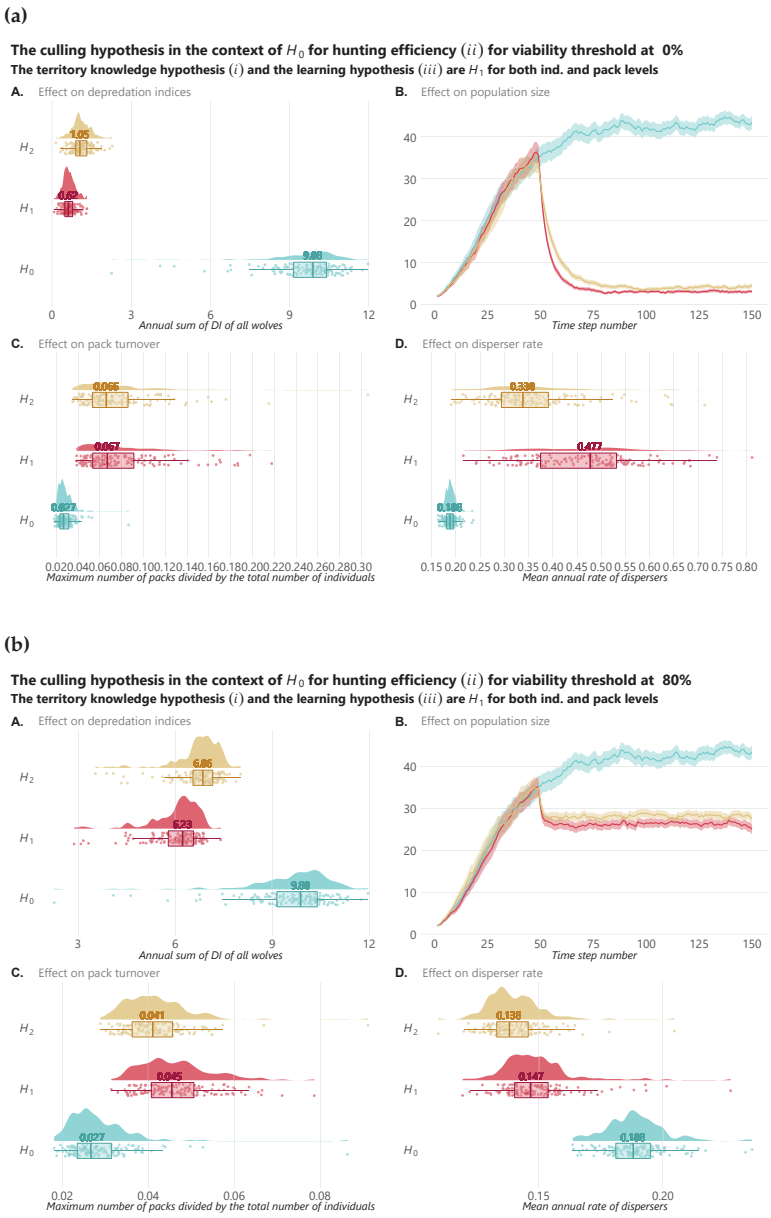

Figure B.5: Dashboard of the effect of the three different culling managements under the context of H_0 for hunting efficiency, and of H_1 for both territory knowledge and learning (for both individual and pack levels) **for a viability threshold of 0% (a) or 80% (b)**. The blue results refer to an absence of culling management, the red results refer to the selective culling management H_1 and the yellow results refer to the random culling management H_2. The culling managements are explained in *The culling scenarios*. Panels A. and D. reflect the results over the time steps period 50-150. For panel B., the ribbon represents the 95% Confidence Interval of the mean. The visualisation of each parameter is explained in greater detail in Table 2.8. Credits: O. Grente

Context 1: vulnerable livestock

This section completes the results when the hunting efficiency hypothesis is considered as H_1 (*Context 1: vulnerable livestock*).

In this context, livestock are considered as more vulnerable than wild preys.Livestock is accessible to wolves regardless their hunting efficiency. However, the range of accessible preys is larger to the most efficient

hunters (adults at the individual level, large packs at the pack level). Theoretically, this should decrease the depredation pressure caused by these wolves compared to the one caused by less efficient hunters (see *Hunting efficiency*).

Configurations for the territory knowledge and learning hypotheses

We present here only the results for which the **viability threshold was 50%**.

The explored configurations are H_0 for both the territory knowledge and learning hypotheses (Figure B.6a), H_1 for the territory knowledge hypothesis and H_0 for the learning hypothesis (Figure B.6b) and H_0 for the territory knowledge hypothesis and H_1 for the learning hypothesis (Figure B.6c).

The scenarios corresponding to these configurations are presented in Table B.2.

(a) Scenarios in Figure B.6a (ind. level)

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE		✓	
PHE	✓		
IL	✓		
PL	✓		
Culling	✓	✓	✓

(b) Scenarios in Figure B.6a (pack level)

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE		✓	
PHE		✓	
IL	✓		
PL	✓		
Culling	✓	✓	✓

(c) Scenarios in Figure B.6b (ind. level)

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE		✓	
PHE	✓		
IL	✓		
PL	✓		
Culling	✓	✓	✓

(d) Scenarios in Figure B.6b (pack level)

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE		✓	
PHE		✓	
IL	✓		
PL	✓		
Culling	✓	✓	✓

(e) Scenarios in Figure B.6c (ind. level)

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE		✓	
PHE	✓		
IL		✓	
PL		✓	
Culling	✓	✓	✓

(f) Scenarios in Figure B.6c (pack level)

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE		✓	
PHE		✓	
IL		✓	
PL		✓	
Culling	✓	✓	✓

Table B.2: The three culling scenarios (last line of each table) analysed under the context of H_1 for hunting efficiency and three different configurations for both territory knowledge and learning, respectively used in Figure B.6a, Figure B.6b and Figure B.6c.

The viability thresholds

Up to now, only the viability threshold of 50% has been used under the context 1 hunting efficiency (H_1). Let's consider now the two other viability thresholds for this context, 0% and 80%. We keep the same

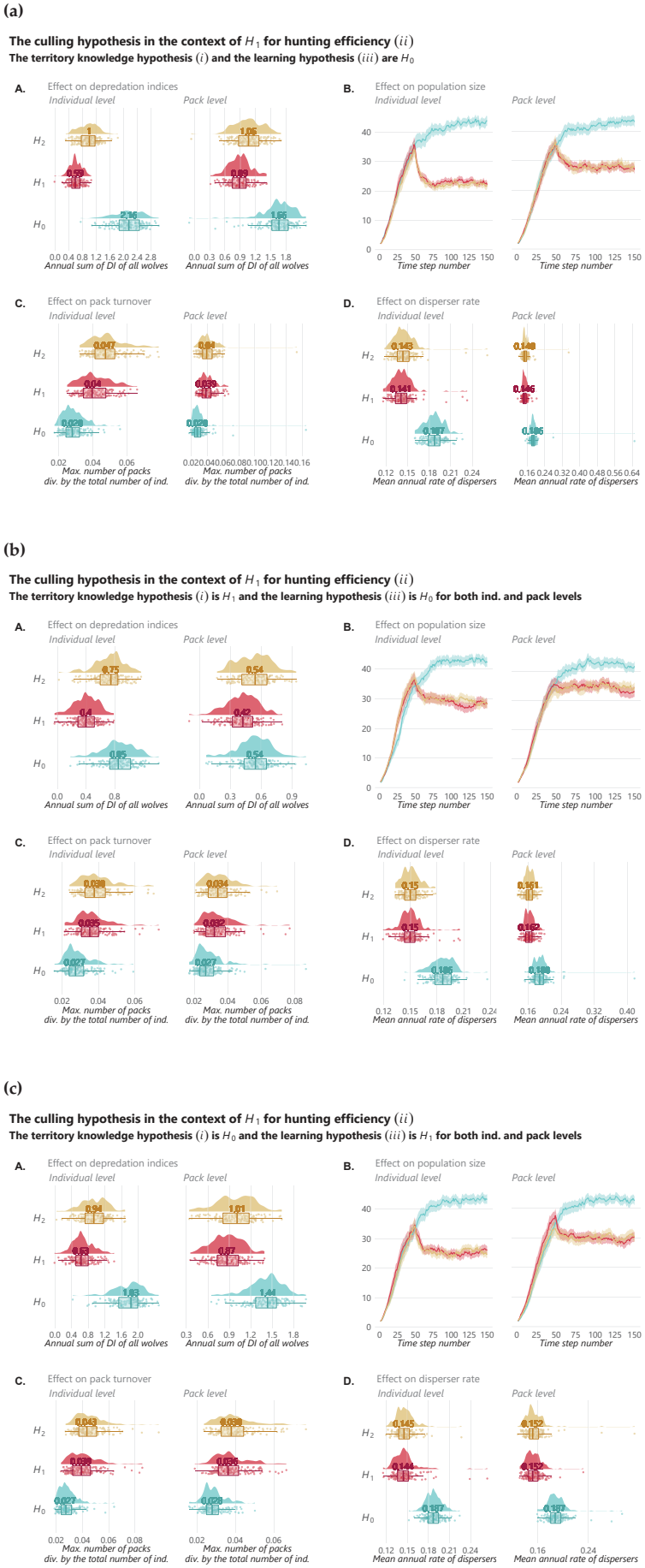

Figure B.6: Dashboard of the effect of the three different culling managements under the context of H_1 for hunting efficiency (at the individual level on the left side of the panels, and at the pack level on the right side of the panels), and three additional configurations for territory knowledge and learning. The blue results refer to an absence of culling management, the red results refer to the selective culling management H_1 and the yellow results refer to the random culling management H_2. The culling managements are explained in *The culling scenarios*. Panels A. and D. reflect the results over the time steps period 50-150. For panel B., the ribbon represents the 95% Confidence Interval of the mean. The visualisation of each parameter is explained in greater detail in Table 2.8. Credits: O. Grente

scenarios as the ones shown in the main text (Table 2.10): the three culling scenarios with H_1 for hunting efficiency and H_1 for both territory knowledge and learning (at both the individual and pack levels).

Under a viability threshold at 0%, this meant that the culling managements were triggered at every time step from the 50th time step, regardless of population size. Under a viability threshold at 80%, this meant that the culling managements could only be triggered if the population exceeded $0.8 \times 50 = 40$ individuals after the Reproduction and Mortality components at the beginning of each time step, from the 50th time step.

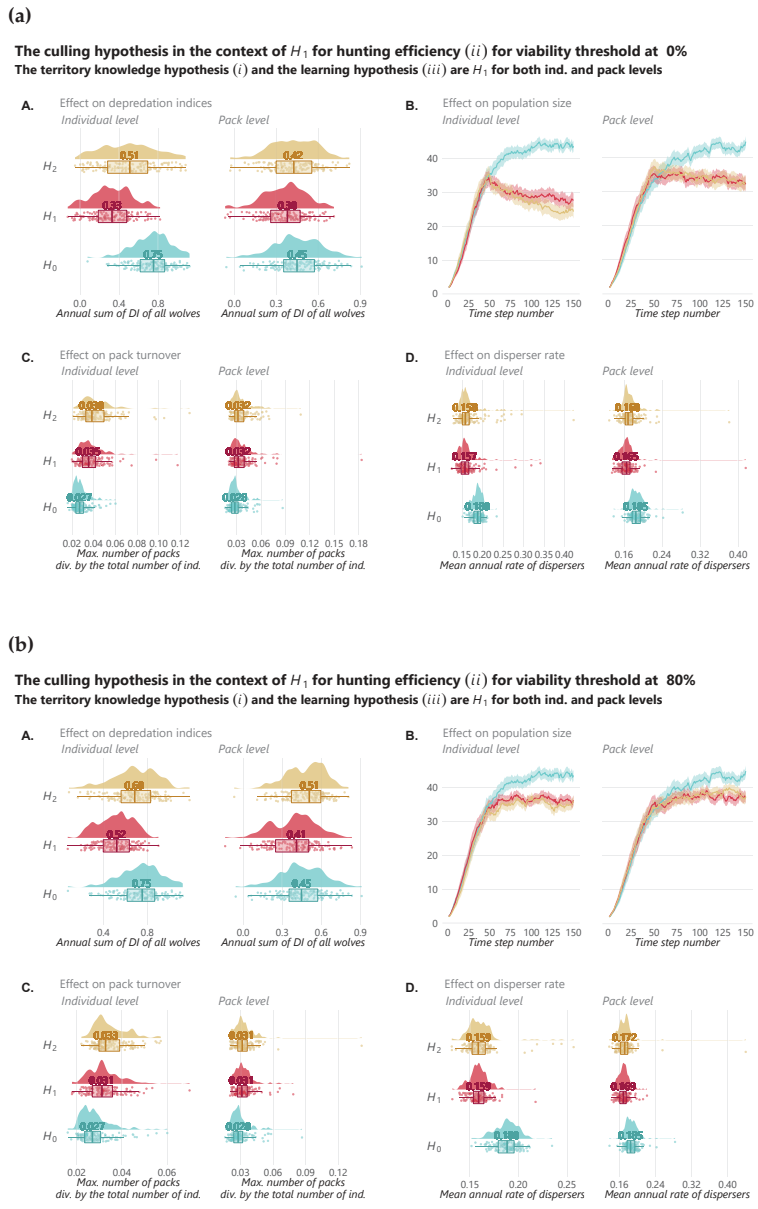

Figure B.7: Dashboard of the effect of the three different culling managements under the context of H_1 for hunting efficiency (at the individual level on the left side of the panels, and at the pack level on the right side of the panels), territory knowledge and learning (for both individual and pack levels) **for a viability threshold of 0% (a) or 80% (b)**. The blue results refer to an absence of culling management, the red results refer to the selective culling management H_1 and the yellow results refer to the random culling management H_2. The culling managements are explained in *The culling scenarios*. Panels A. and D. reflect the results over the time steps period 50-150. For panel B., the ribbon represents the 95% Confidence Interval of the mean. The visualisation of each parameter is explained in greater detail in Table 2.8. Credits: O. Grente

Context 2: highly protected livestock

This section completes the results when the hunting efficiency hypothesis is considered as H_2 (*Context 2: highly protected livestock*).

In this context, livestock are considered as less vulnerable than wild preys. Livestock is accessible to the best hunters amongst wolves (adults or large packs). Therefore, their risk of depredation is increased compared to less efficient hunters in this context.

Configurations for the territory knowledge and learning hypotheses

We present here only the results for which the **viability threshold was 50%**.

The explored configurations are H_0 for both the territory knowledge and learning hypotheses (Figure B.8a), H_1 for the territory knowledge hypothesis and H_0 for the learning hypothesis (Figure B.8b) and H_0 for the territory knowledge hypothesis and H_1 for the learning hypothesis (Figure B.8c).

The scenarios corresponding to these configurations are presented in Table B.3.

Table B.3: The three culling scenarios (last line for each table) analysed under the context of H_2 for hunting efficiency and three different configurations for both territory knowledge and learning, respectively used in Figure B.8a, Figure B.8b and Figure B.8c.

(a) Scenarios in Figure B.8a (ind. level)

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE			✓
PHE	✓		
IL	✓		
PL	✓		
Culling	✓	✓	✓

(b) Scenarios in Figure B.8a (pack level)

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE			✓
PHE			✓
IL	✓		
PL	✓		
Culling	✓	✓	✓

(c) Scenarios in Figure B.8b (ind. level)

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE			✓
PHE	✓		
IL	✓		
PL	✓		
Culling	✓	✓	✓

(d) Scenarios in Figure B.8b (pack level)

Hypothesis	H_0	H_1	H_2
ITK		✓	
PTK		✓	
IHE			✓
PHE			✓
IL	✓		
PL	✓		
Culling	✓	✓	✓

(e) Scenarios in Figure B.8c (ind. level)

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE			✓
PHE	✓		
IL		✓	
PL		✓	
Culling	✓	✓	✓

(f) Scenarios in Figure B.8c (pack level)

Hypothesis	H_0	H_1	H_2
ITK	✓		
PTK	✓		
IHE			✓
PHE			✓
IL		✓	
PL		✓	
Culling	✓	✓	✓

The viability thresholds

Up to now, only the viability threshold of 50% has been used under the context 2 of hunting efficiency (H_2). Let's consider now the two other viability thresholds for this context, 0% and 80%. We keep the

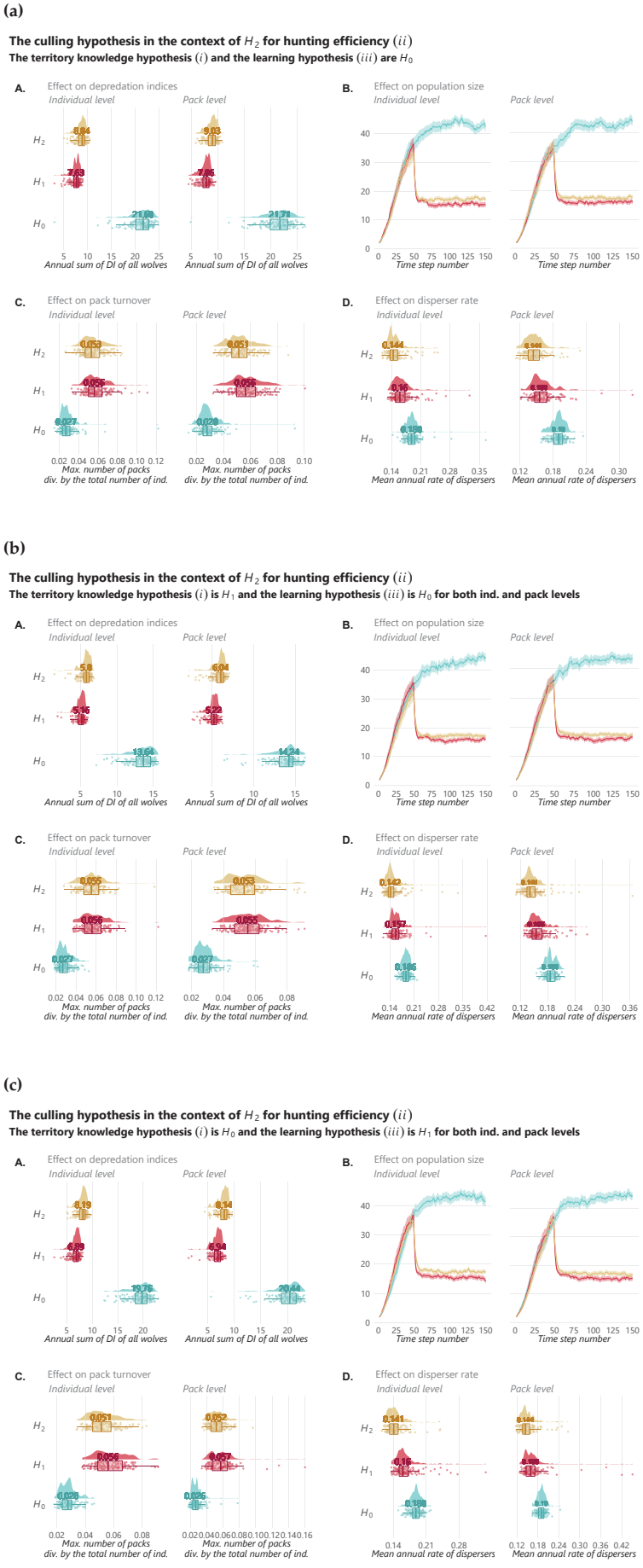

Figure B.8: Dashboard of the effect of the three different culling managements under the context of H_2 for hunting efficiency (at the individual level on the left side of the panels, and at the pack level on the right side of the panels), and three additional configurations for territory knowledge and learning. The blue results refer to an absence of culling management, the red results refer to the selective culling management H_1 and the yellow results refer to the random culling management H_2. The culling managements are explained in *The culling scenarios*. Panels A. and D. reflect the results over the time steps period 50-150. For panel B., the ribbon represents the 95% Confidence Interval of the mean. The visualisation of each parameter is explained in greater detail in Table 2.8. Credits: O. Grente

same scenarios as the ones shown in the main text (Table 2.11): the three culling scenarios with H_2 for hunting efficiency and H_1 for both territory knowledge and learning (at both the individual and pack levels).

Under a viability threshold at 0%, this meant that the culling managements were triggered at every time step from the 50th time step, regardless of population size. Under a viability threshold at 80%, this meant the culling managements could only be triggered if the population exceeded $0.8 \times 50 = 40$ individuals after the Reproduction and Mortality components at the beginning of each time step, from the 50th time step.

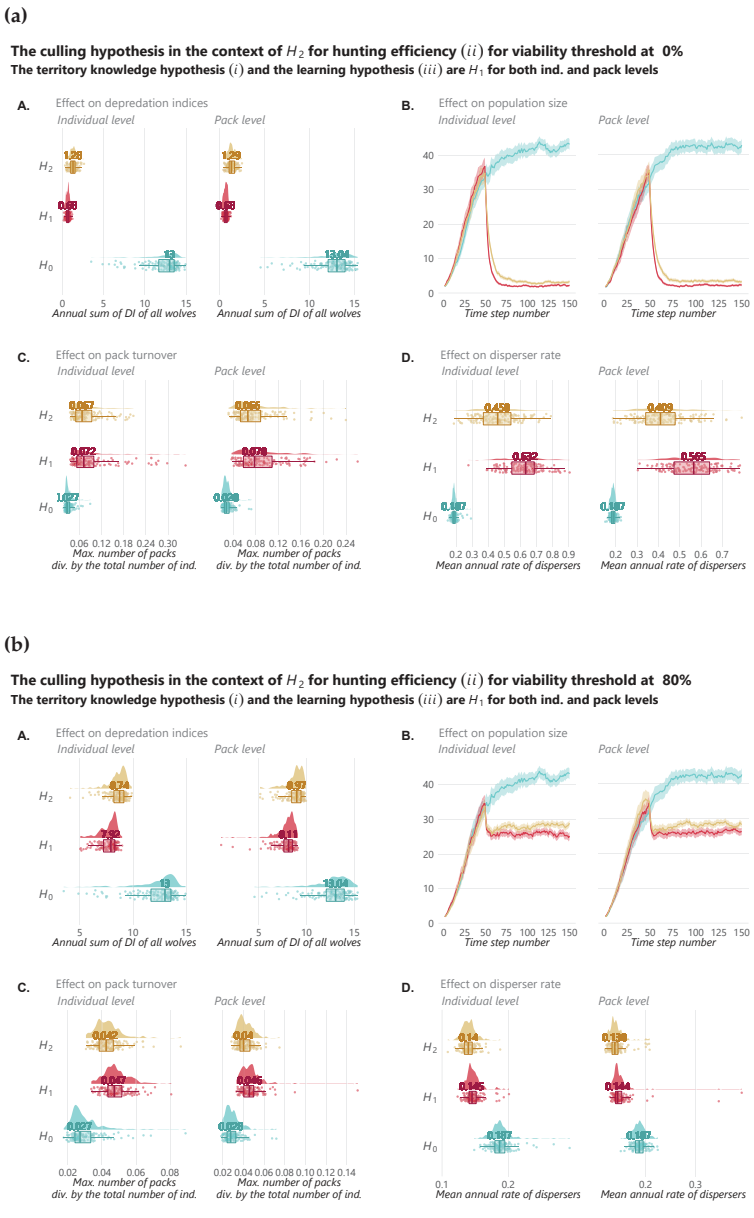

Figure B.9: Dashboard of the effect of the three different culling managements under the context of H_2 for hunting efficiency (at the individual level on the left side of the panels, and at the pack level on the right side of the panels), and H_1 for territory knowledge and learning (for both individual and pack levels) **for a viability threshold of 0% (a) or 80% (b)**. The blue results refer to an absence of culling management, the red results refer to the selective culling management H_1 and the yellow results refer to the random culling management H_2. The culling managements are explained in *The culling scenarios*. Panels A. and D. reflect the results over the time steps period 50-150. For panel B., the ribbon represents the 95% Confidence Interval of the mean. The visualisation of each parameter is explained in greater detail in Table 2.8. Credits: O. Grente

Effects of culling on depredation

C

This appendix completes Chapter 3 (Effects of culling on depredation) on page 127.

C.1 Correction for seasonality 300
Method 1: restriction of the temporal buffer 300
Method 2: estimated pastoral dynamic 301
Method 3: estimated seasonal dynamic without culling 301
C.2 Complement for results on operations 303

C.1 Correction for seasonality

Method 1: restriction of the temporal buffer

This section refers to section 12 (Method 1: restriction of the temporal buffer) on page 160, where the temporal buffer was shorten to 40 days instead of 180 days. These are the results when no outlier correction was applied. Here, the outliers in the depredation density distribution were flattening the results because of unbalanced spatial correction, therefore a methodological bias. This result is given for information and transparency, but we strongly recommend to focus on Figure 3.30 where an outlier correction is applied.

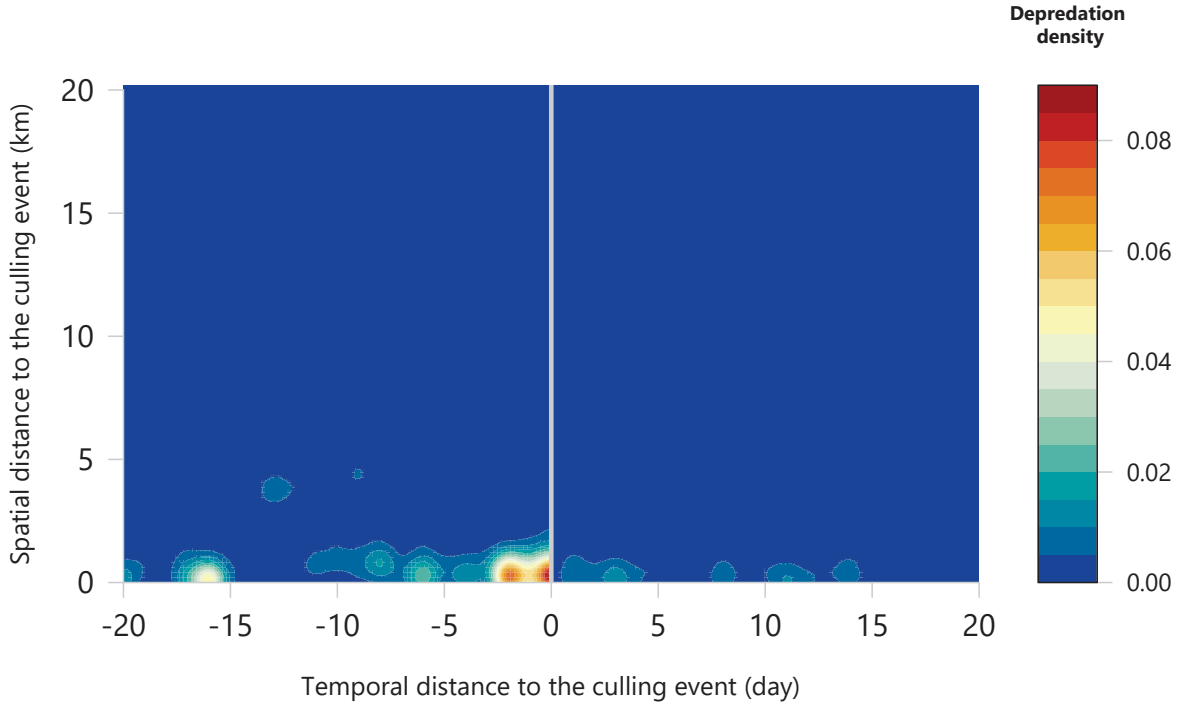

Figure C.1: Estimation of the depredation density per unit of time and space around the 252 unique culling events with a temporal buffer of 40 days. The depredation density of a unit was defined in Definition 4. The depredations involved in the analysis were found inside the pastures partially or integrally overlapping the circle of 10 km radius around the culling events. Depredations were therefore scarcer above 10 km from the culling events, as the pastures were generally not spread out over large distances outside the circle of 10 km radius. Credits: O. Grente

Method 2: estimated pastoral dynamic

This section refers to section 12 (Method 2: estimated pastoral dynamic) on page 162, where the depredation intensity was corrected with an estimated pastoral intensity. These are the results of the standard deviation of the depredation density for 1000 sets of simulated depredations for the 236 unique culling events.

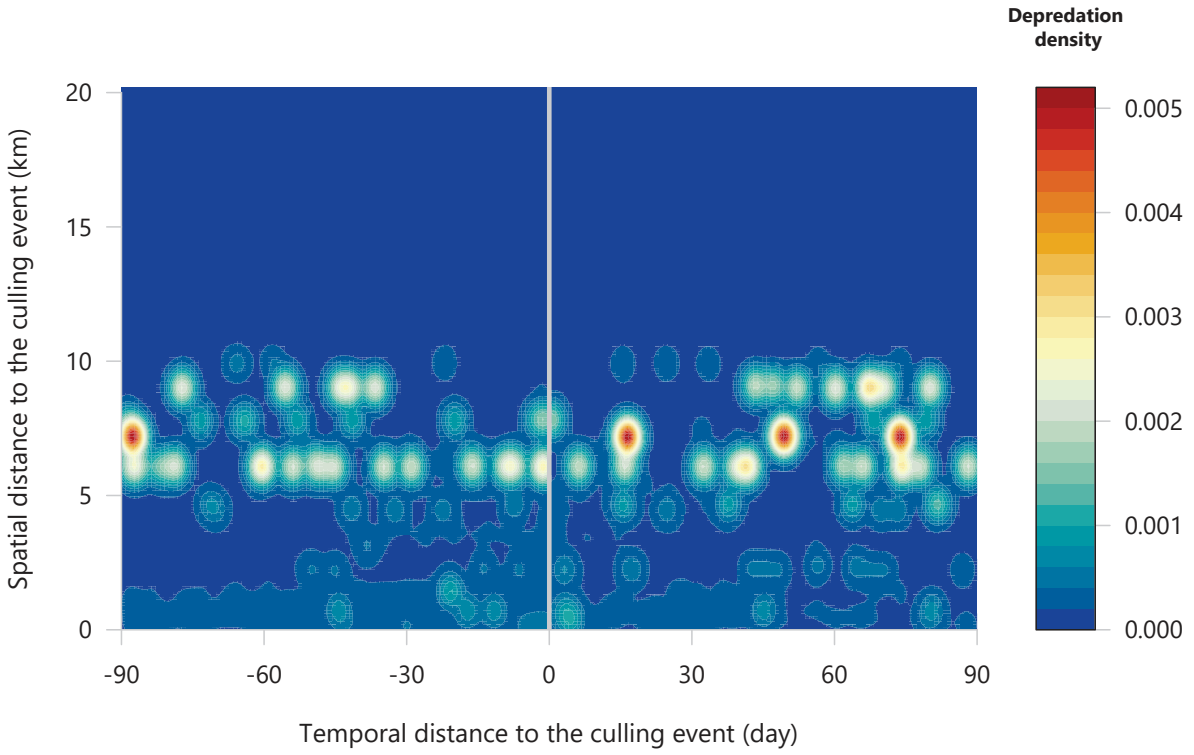

Figure C.2: Estimation of the standard deviation of depredation density for the 236 unique culling events when simulating 1000 sets of depredations spatially and temporally located according to the pastoral use. Credits: O. Grente

Method 3: estimated seasonal dynamic without culling

This section refers to section 12 (Method 3: estimated seasonal dynamic without culling) on page 166, where the depredation intensity without culling was estimated through the selection of non-culling events, each non-culling event involving equivalent confounding factors to those of the observed set of 227 unique culling events retained for this analysis (located in or near a delimited massif from Figure 3.34).

Figure C.3 is the results of the standard deviation of the depredation density for 100 sets of 227 non-culling events.

Figure C.4 is the results of the mean of the depredation density for 100 sets of 227 non-culling events when no outlier correction was applied.

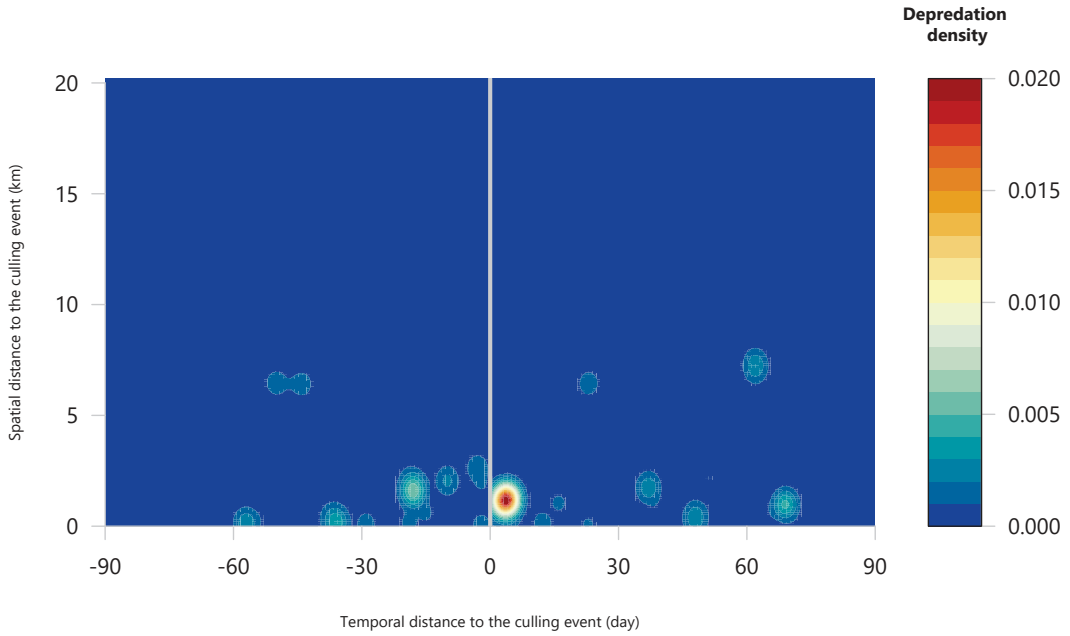

Figure C.3: Estimation of the standard deviation of depredation density for 100 sets of 227 non-culling events. Each set of 227 non-culling events was selected to involve equivalent confounding factors to those of the observed set of 227 unique culling events. Credits: O. Grente

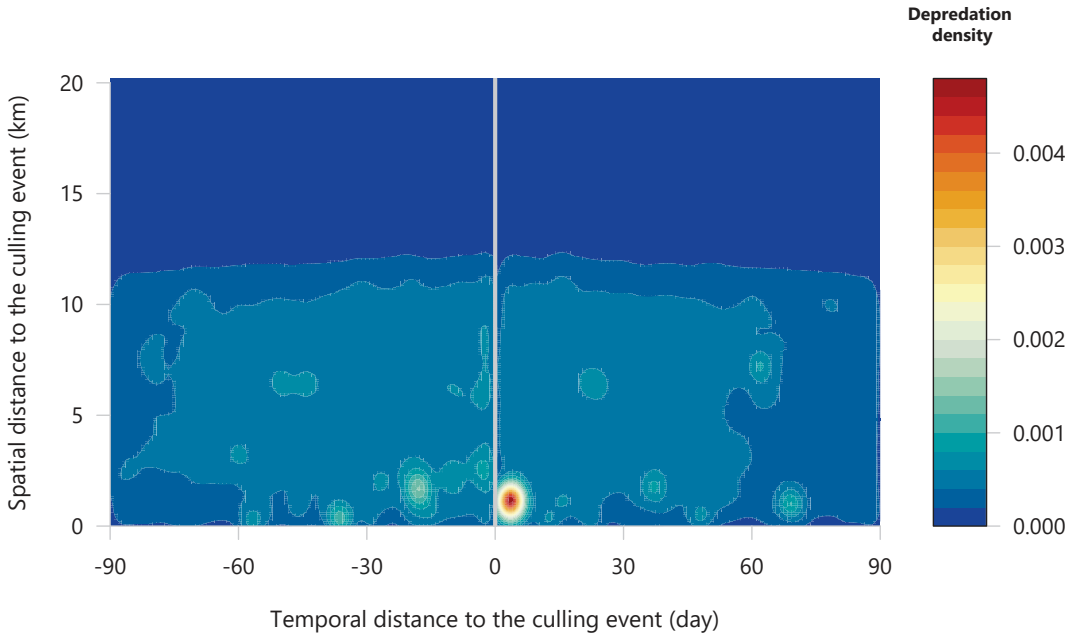

Figure C.4: Estimation of the mean depredation density for 100 sets of 227 non-culling events, without outlier correction. Each set of 227 non-culling events was selected to involve equivalent confounding factors to those of the observed set of 227 unique culling events. Credits: O. Grente

C.2 Complement for results on operations

This section refers to section 16 (Operations of *brigadiers*) on page 189, where the depredation intensity before and after operations of *brigadiers* was analysed. I display here the results for operations according to their results: successful shot, missed shot or no shot.

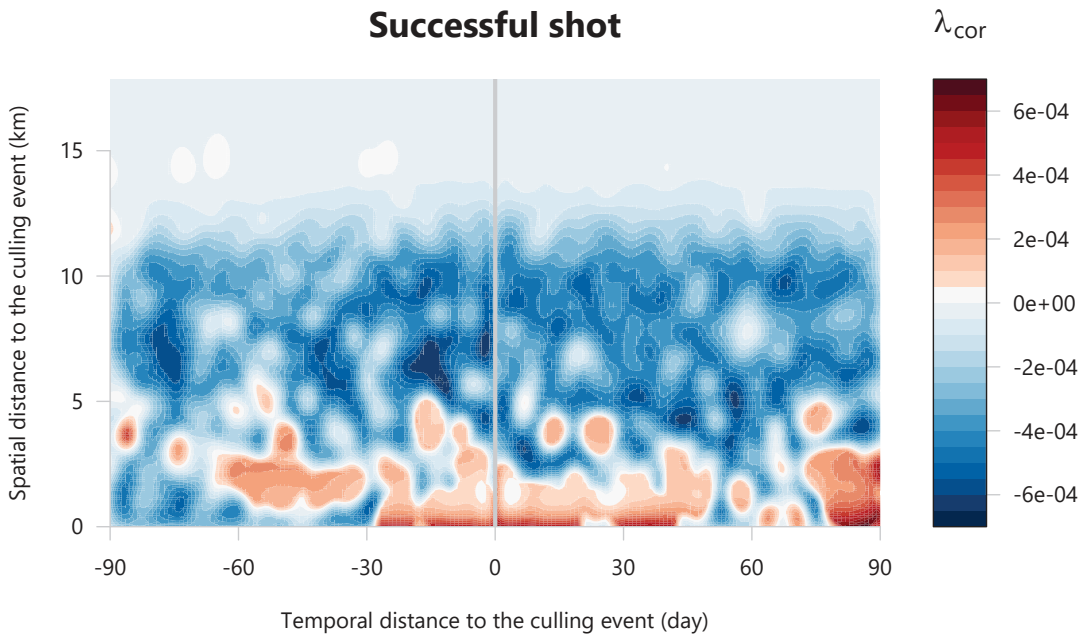

Figure C.5: Depredation density corrected by pastoral use for the 21 operations with at least one successful shot. The buffers of these operations encompassed on average 63 depredations ($sd = 27$) for a total of 1 320 depredations. Credits: O. Grente

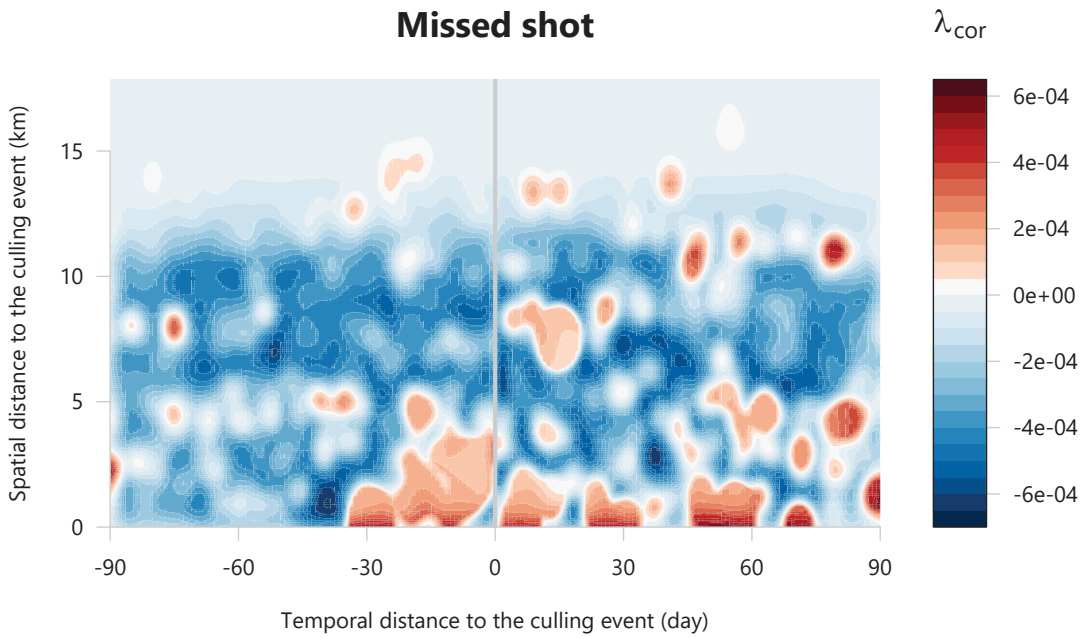

Figure C.6: Depredation density corrected by pastoral use for the 19 operations with missed shot(s). The buffers of these operations encompassed on average 50 depredations ($sd = 31$) for a total of 946 depredations. Credits: O. Grente

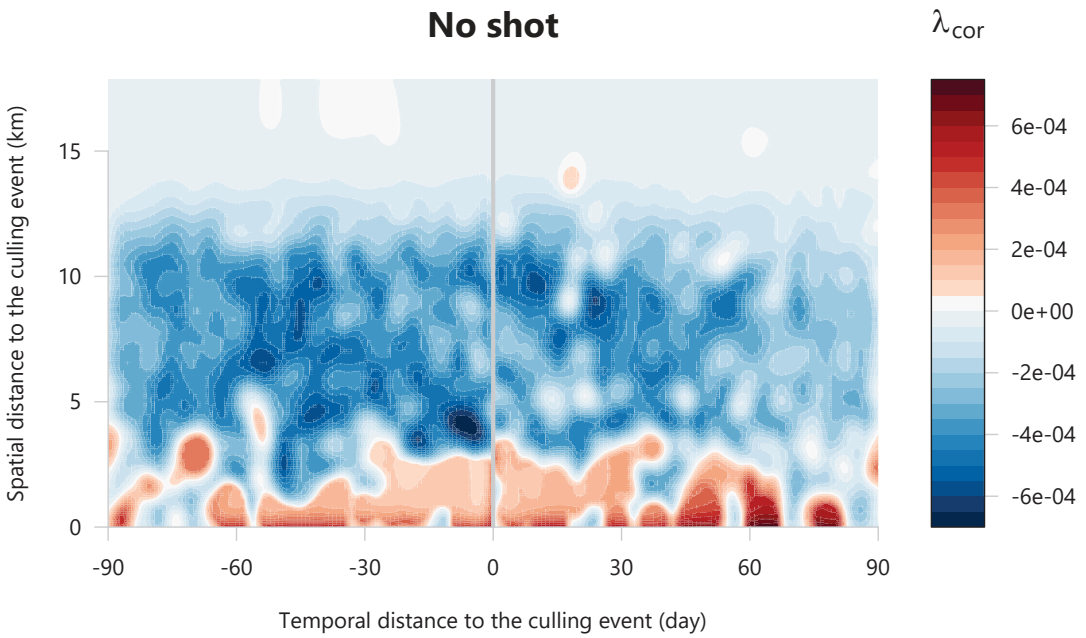

Figure C.7: Depredation density corrected by pastoral use for the 38 operations without shot but with wolf observation. The buffers of these operations encompassed on average 61 depredations (sd = 28) for a total of 2 335 depredations. Credits: O. Grente

Hotspots of depredation | D

This appendix completes Chapter 4 (Hotspots of depredation) on page 203.

D.1 Interactive figures with R-Shiny 305

D.1 Interactive figures with R-Shiny



The results from Chapter 4 included maps and figures. Most of the time, results had to be displayed for each analysed year from the period 1995-2018. We used *flexdashboard* and *Shiny* in R.4.0.2 [193] to create interactive figures where the visualisation of the annual results is facilitated by a slider. These figures are displayed online and can be accessed from any computer thanks to an Internet connection by clicking on the links below.

Figure D.1: Pastoral information of the study area, from the census of 1996-1997 and from the census of 2012-2014. Available here: https://oksanagrente.shinyapps.io/Hotspots-SuppFig1/

Figure D.2: Annual distributions of wolf presence, pastoral surfaces and verified wolf depredations on sheep in the study area between biological years 1995 and 2018. Available here: https://oksanagrente.shinyapps.io/Hotspots-SuppFig2/

Figure D.3: Annual distributions of the number of wolf depredations on sheep per pastoral surface, at the regional and local scales between biological years 1995 and 2018. Available here: https://oksanagrente.shinyapps.io/Hotspots-SuppFig3/

Figure D.4: Annual results between biological years 1995 and 2018 of the K_{inhom} analysis and of the two K analyses (one with the analysis grid simulated over the pastoral surfaces at depredation risk, the other only over the wolf distribution) at the regional and local scales. Available here: https://oksanagrente.shinyapps.io/Hotspots-SuppFig4/

Figure D.5: Annual locations between biological years 1995 and 2018 of depredated pastoral surfaces identified or not as hotspots, according to the Kulldorff statistic used with the observed heterogeneous sheep availability or the simulated homogeneous sheep availability at the regional scale. Available here: https://oksanagrente.shinyapps.io/Hotspots-SuppFig5/

Communication article | E

This appendix is mentioned in Chapter 5 (Discussion) on page 223, and contains the full article of:

> Oksana Grente, Christophe Duchamp, Nolwenn Drouet-Hoguet, Sarah Bauduin, Thomas Opitz, Simon Chamaillé-Jammes and Olivier Gimenez (2020). Tirs dérogatoires de loups en France : état des connaissances et des enjeux pour la gestion des attaques aux troupeaux. *Faune Sauvage*, Number 327, p.16-21.

This article in French communicates about the objectives of the PhD thesis, the gaps in the literature review and the methods that were intended to be used for the studies of the PhD thesis. It has been published in *Faune Sauvage*, a journal of communication about the activities and research conducted at the Office National de la Chasse et de la Faune Sauvage (ONCFS) which became Office Français de la Biodiversité (OFB) since 2020.

The article has also been released in the national website *Loupfrance* managed by OFB about the wolf situation in France here.

The article is not peer-reviewed by the scientific community.

Erratum: In the article, it is wrongly mentioned that [96] and [52] used an *intra-site* comparison. They in fact used an *inter-site* comparison. A detailed synthesis of these studies is provided in section *Literature review* of Chapter 3.

[96]: Bradley et al. (2015), 'Effects of Wolf Removal on Livestock Depredation Recurrence and Wolf Recovery in Montana, Idaho, and Wyoming'

[52]: Santiago-Avila et al. (2018), 'Killing Wolves to Prevent Predation on Livestock May Protect One Farm but Harm Neighbors'



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Tirs dérogatoires de loups en France : état des connaissances et des enjeux pour la gestion des attaques aux troupeaux

▲ *Loup gris dans les Pyrénées.*

En France, la protection des troupeaux contre les attaques de loup prévoit l'utilisation de tirs dérogatoires dans des contextes précis, notamment lorsque la pression des attaques est forte. Néanmoins, les effets de ces tirs sur les attaques restent mal connus. Nous dressons ici un état des connaissances scientifiques sur le sujet puis présentons les enjeux et le cadre méthodologique de l'étude en cours, qui s'attache à évaluer les effets des tirs dérogatoires sur les attaques et la population de loups en France.

Oksana Grente[1,2], Christophe Duchamp[1], Sarah Bauduin[1], Thomas Opitz[3], Simon Chamaillé-Jammes[2], Nolwenn Drouet-Hoguet[1*], Olivier Gimenez[2*]

[1] OFB, Direction de la recherche et de l'appui scientifique, Unité Prédateurs, animaux déprédateurs et exotiques, Équipe Loup et Lynx – Gières.
[2] CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Univ. Paul Valéry Montpellier 3 – Montpellier.
[3] INRAE – Avignon.
** Les deux auteurs ont équitablement supervisé le projet.*

Contact : nolwenn.drouet-hoguet@ofb.gouv.fr

La gestion de la population de loups en France

Le retour du loup (*Canis lupus*) en France au début des années 1990 s'est accompagné d'attaques (ou « déprédations ») sur les troupeaux domestiques, notamment dans les massifs à forte valeur pastorale ovine. Pour prendre en compte cette contrainte environnementale, l'État indemnise les dommages sur les troupeaux domestiques imputés au loup et subventionne la mise en place de mesures de protection des troupeaux. Depuis 2004, cette stratégie est définie dans un Plan national d'actions (PNA), actualisé à trois reprises[1].

1. Le PNA 2018-2023 sur le loup et les activités d'élevage peut être téléchargé *via* https://bit.ly/2AAnOGz.

Classé en Annexe IV de la directive européenne « Habitats-Faune-Flore » que la France a ratifiée, le loup est une espèce strictement protégée et il est interdit de lui nuire, même pour limiter la déprédation. Toutefois, la directive européenne prévoit la possibilité de déroger au statut de protection de l'espèce sous certaines conditions. Ces dérogations sont encadrées en France par un arrêté ministériel qui autorise le prélèvement par le tir d'un nombre de loups défini chaque année, seulement dans les situations jugées les plus difficiles pour les éleveurs.

Dans le même temps, l'État français doit garantir un état de conservation favorable de l'espèce, compte tenu de ses engagements européens. Les actions de gestion telles que les tirs dérogatoires ne doivent pas nuire à la viabilité de la population de

loups, tout en réduisant les dommages aux troupeaux. Si la viabilité de la population de loups en France a été mesurée par l'expertise collective de 2017 (Duchamp *et al.*, 2017), l'efficacité du contrôle létal de grands prédateurs à réduire les dommages est plus difficile à évaluer et fait actuellement débat parmi les scientifiques (Lute *et al.*, 2018). Après plusieurs années de pratique de ce dispositif, et conformément aux attentes de l'action 7.5 du PNA 2018-2023, une étude a démarré en 2018 sous la forme d'une thèse de doctorat OFB-CNRS, afin d'évaluer l'effet de ces tirs dérogatoires sur la déprédation due au loup en France.

Que sait-on au sujet du contrôle létal des populations de loups et de ses effets sur la déprédation ?

Quels liens entre contrôle létal et déprédation ?

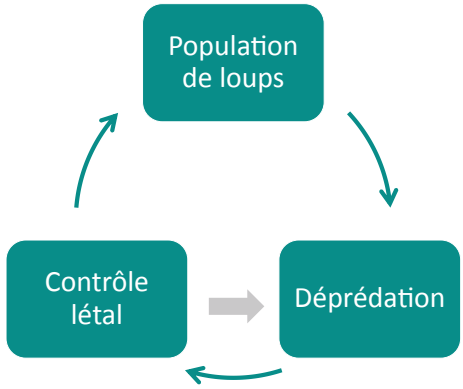
Deux théories existent sur le sujet (Treves *et al.*, 2019). La première théorie argumente que le contrôle létal permettrait d'éliminer les loups potentiellement spécialisés dans la déprédation, de réduire localement l'abondance du prédateur et de rendre les loups survivants plus méfiants envers l'humain et ses troupeaux (Meuret *et al.*, 2018). Les risques de rencontres entre prédateurs et bétail s'en trouveraient abaissés, et par conséquent ceux de déprédation également. L'autre théorie avance que le contrôle létal, en prélevant notamment les loups reproducteurs, pourrait déstabiliser, voire dissoudre les meutes et provoquer une réorganisation des territoires. Les loups en dispersion dépourvus de leurs congénères, ou ceux nouvellement arrivés sans connaissance préalable du territoire, pourraient alors se rabattre sur les troupeaux domestiques, plus repérables et plus vulnérables que les proies sauvages (Imbert *et al.*, 2016).

C'est donc à travers la modification de la population de loups que le contrôle létal peut avoir un effet sur la déprédation. Les changements induits dans la déprédation peuvent en retour agir sur l'application initiale du contrôle létal. L'ensemble de la problématique peut alors être envisagé sous la forme d'un cycle (***figure 1***). Cependant, il a été beaucoup plus courant jusqu'ici d'étudier directement l'effet du contrôle létal sur les niveaux d'attaques constatés en réponse, plutôt que ce cycle dans sa globalité.

Peu d'études, et des protocoles d'analyse à revoir

Plus d'une quinzaine de revues bibliographiques sur la thématique du contrôle létal appliqué aux grands prédateurs existe dans la littérature scientifique (exemples : Miller *et al.*, 2016 ; Lennox *et al.*, 2018 ; Treves *et al.*, 2019). Ces travaux s'accordent sur le manque d'études qui analysent l'effet du contrôle létal sur les niveaux de déprédation, quels que soient le type de contrôle et l'espèce visée. Actuellement, à peine une dizaine d'articles scientifiques dans le monde a analysé l'effet du contrôle létal sur les niveaux d'attaques de *Canis lupus*. De plus, toutes ces études ont été réalisées en Amérique du Nord, à l'exception d'une étude en Espagne (Fernández-Gil *et al.*, 2016).

Figure 1 **Modèle de cycle de l'effet du contrôle létal sur les niveaux d'attaques par l'intermédiaire d'une modification de la population de loups.** La flèche grise symbolise l'axe d'étude couramment employé dans la littérature, qui consiste à étudier directement l'effet du contrôle létal sur les niveaux d'attaques.

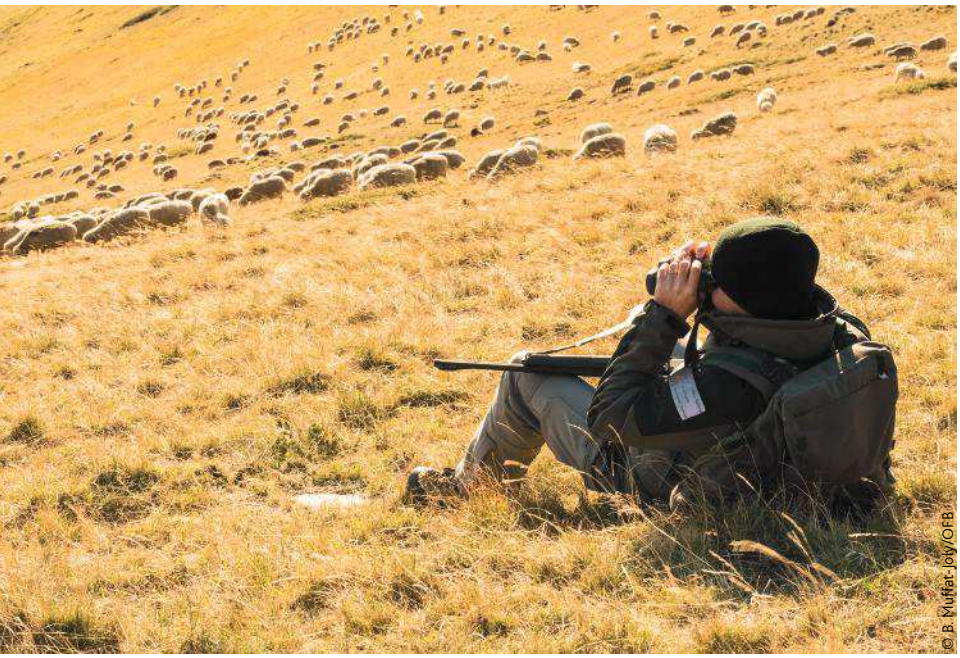


Ces revues insistent également sur la faiblesse des protocoles d'analyse employés, tous prédateurs confondus. Peu d'études utilisent un protocole expérimental, initialement mis en place avec un choix aléatoire de zones tests où serait appliqué le contrôle létal, et des zones sans contrôle létal. Ce type de mise en place expérimentale est en effet peu adapté au statut des espèces protégées, qui ne permet pas de faire varier les différents niveaux de prélèvement.

En grande majorité donc, les études procèdent à une analyse rétrospective des données issues de contrôle létal déjà mis en place dans le cadre d'une gestion, et non pas selon un protocole scientifique établi au préalable (Treves *et al.*, 2019).

Ces études comparent des zones où le contrôle létal a été appliqué et d'autres où il ne l'a pas été, ou bien comparent les situations avant et après l'application d'un contrôle létal dans une même zone. Cependant, ces études risquent d'attribuer au contrôle létal les fluctuations observées dans les niveaux de déprédation, alors que celles-ci peuvent être dues à d'autres différences entre les exploitations agricoles (environnementales, pastorales…) ou au sein d'un même pâturage au cours du temps (Treves *et al.*, 2019).

Enfin, d'autres études rétrospectives cherchent plutôt à établir un lien direct entre les niveaux de déprédation et la quantité de prédateurs prélevés, en adoptant une approche corrélative. Celles-ci ne permettent pas de distinguer la cause de l'effet, ce qui peut conduire à des interprétations erronées. Plus faciles d'application en termes d'analyse, elles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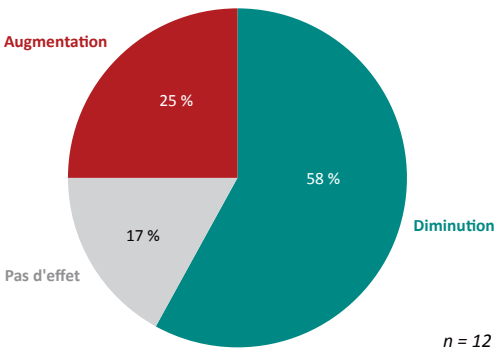
▲ *Agent de la Brigade mobile d'intervention « Loup* » en opération de protection de troupeau.*
* https://www.loupfrance.fr/gestion-des-impacts-du-loup/brigade-mobile-d-intervention-loup

sont surreprésentées, et celles qui se penchent sur le loup ne font pas exception puisqu'elles en représentent les deux tiers. Le tiers restant est composé d'études rétrospectives non corrélatives, aucune étude sur le loup n'étant expérimentale à ce jour.

Des études aux conclusions contradictoires

La faiblesse des protocoles d'analyse employés conduit à des conclusions divergentes (***figure 2***), parfois pour un même jeu de données d'attaques et de prélèvements. C'est le cas pour trois études corrélatives qui analysent vingt-cinq ans de données dans les états américains de l'Idaho, du Montana et du Wyoming (Wielgus & Peebles, 2014 ; Poudyal *et al*., 2016 ; Kompaniyets & Evans, 2017). L'étude de 2017, qui corrige les biais méthodologiques des études de 2014 et 2016, conclut que durant la phase de recolonisation du loup, le nombre de déprédations augmente malgré l'application du contrôle létal. Pendant cette période, la croissance de la population excède les prélèvements, ce qui a pour effet d'augmenter les effectifs de loups. Cette croissance populationnelle peut alors naturellement expliquer la hausse du nombre d'attaques selon les auteurs. Au contraire, Wielgus & Peebles (2014) identifiaient le contrôle létal comme la cause directe de l'augmentation du nombre de dommages, car ils omettaient d'intégrer la croissance de la population de loups dans leurs analyses, les conduisant à une erreur d'interprétation. Kompaniyets & Evans (2017) concluent d'ailleurs que lorsque la phase de recolonisation laisse place à celle de stabilisation, au cours de laquelle la population de loups n'augmente plus, alors le contrôle létal a pour effet de diminuer le nombre de déprédations.

Figure 2 **Répartition des effets du contrôle létal sur les niveaux de déprédation identifiés par 12 analyses scientifiques.**
Effet d'augmentation sur le niveau de déprédation du loup après contrôle (rouge), effet de diminution (vert), ou aucun effet (gris).




© Réseau Loup-Lynx

▲ *Consommation d'un ovin par un loup. Cliché de piège photographique posé par un berger à la suite d'une attaque de loup sur son troupeau en alpage dans les Hautes-Alpes.*

Les études non corrélatives mais rétrospectives ne permettent pas non plus de trancher sur la problématique. En comparant des fermes qui subissent des attaques de loup dans le Minnesota, Harper *et al*. (2008) démontrent que le piégeage d'un loup mâle adulte réduit le risque de réapparition des attaques de loup dans les fermes piégées par rapport à celles qui ne le sont pas. Cependant, cette réduction reste faible et est également observée lorsque le piège est posé mais qu'aucun loup n'est capturé. Dans une comparaison de la situation avant et après le contrôle létal sur le territoire de meutes dans les Rocheuses américaines, Bradley *et al*. (2015) notent que le contrôle létal permet d'allonger significativement le délai avant l'attaque suivante sur un même territoire. Enfin, Santiago-Avila *et al*. (2018) observent dans le Michigan une tendance à la baisse du risque de réapparition d'une attaque de loup à la suite du contrôle létal, sur une superficie d'environ 3 km² centrée sur l'attaque initiale. En revanche, ils observent une tendance à la hausse de ce risque lorsque l'analyse est faite à une plus grande échelle, sur 90 km², traduisant un report potentiel des attaques sur les troupeaux voisins. Cependant, ces deux tendances restent faibles et ne sont pas statistiquement significatives.

Des échelles d'analyse spatiales et temporelles limitées ou inadaptées

Les études citées sur le loup évaluent souvent les effets du contrôle létal seulement lorsque qu'un certain laps de temps s'est écoulé, par exemple un an après le contrôle (Kompaniyets & Evans, 2017), plutôt que de façon continue tout au long de l'année après le contrôle (Santiago-Avila *et al*., 2018).

De plus, les échelles spatiales analysées sont souvent inappropriées aux rythmes et aux mouvements des animaux dans leurs territoires. Beaucoup d'études analysent le phénomène à des échelles supérieures à 1 000 km², ou bien n'analysent pas les risques de report de la déprédation sur les fermes voisines, à l'exception de Santiago-Avila *et al*. (2018).

Comment mesurer les effets des tirs dérogatoires en France pour la gestion des dégâts aux troupeaux ?

La situation en France est différente de celle qui a cours en Amérique du Nord, notamment en ce qui concerne les pratiques pastorales et le dispositif lié au contrôle létal. Une étude spécifique au contexte français est donc nécessaire. Jusqu'à présent, deux rapports se sont penchés sur la situation française. Dans le Parc naturel régional du Queyras, Plisson (2011) n'identifie aucune corrélation entre la réalisation de tirs de défense et/ou d'effarouchement et le risque qu'un quartier d'unité pastorale subisse une attaque de loup dans la semaine qui suit ces tirs. En revanche, Le Cam (2012) montre, lors d'une analyse nationale couvrant la période 2009-2011, que le nombre d'attaques de loup sur un troupeau baisse significativement pendant une semaine une fois que la dérogation de tir visant à le protéger entre en vigueur, indépendamment de la mort d'un loup. Ces résultats rejoignent ceux de Harper *et al*. (2008) sur l'effet de dissuasion d'une présence humaine renforcée. Le Cam (2012) démontre également que les troupeaux voisins bénéficient aussi de cette baisse à très court terme, mais sans effet sur le long terme.

Finalement, comme sur le plan international, les effets du contrôle létal sur la population de loups restent encore méconnus en France. La thèse a pour objectif d'évaluer ces effets et s'appuie sur les données des sept dernières années de mise en œuvre des tirs dérogatoires réalisés en France. Ces données, essentiellement issues du massif alpin, concernent les prélèvements de loups tués par un tir dérogatoire. En raison des lacunes identifiées sur la problématique grâce à la revue

bibliographique, quatre points clés ont été identifiés pour que l'étude adopte la méthodologie la plus robuste possible.

Un protocole avant/après pour évaluer l'effet des tirs létaux sur les niveaux de déprédation

L'utilisation de données déjà collectées permet de réaliser une étude, non pas expérimentale, mais rétrospective. Parmi les approches rétrospectives possibles, la comparaison « intra-site » a été préférée (c.-à-d. avant *vs* après l'application du tir au sein du même site) plutôt que la comparaison « inter-site » (c.-à-d. entre des sites avec tir *vs* sans tir). En effet, si une situation environnementale ou pastorale peut changer au cours du temps, affaiblissant alors l'analyse, on s'attend cependant à ce que ces variations soient moins élevées que les différences entre plusieurs pâturages.

La nécessaire prise en compte des échelles spatiales et temporelles

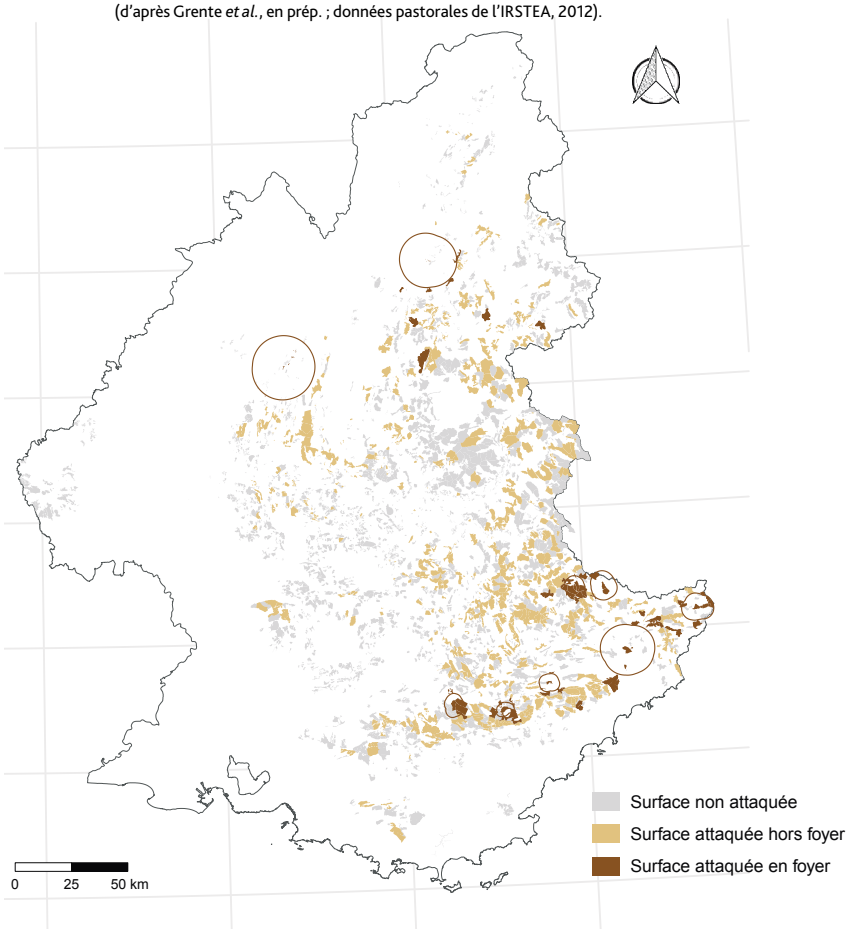
L'un des enjeux de l'étude concerne l'identification des « bonnes » échelles spatiales et temporelles auxquelles se produisent les effets des tirs. Dans un premier temps, il a été nécessaire de comprendre à quelles échelles définir les foyers de déprédation (***figure 3***)[2]. Dans un second temps, afin de ne pas négliger les potentiels reports de déprédation sur les autres pâturages, le principe sera d'analyser les effets des tirs sur les niveaux d'attaques le long d'un gradient spatial et temporel autour des tirs, dans un rayon d'action que l'analyse précédente aura aidé à définir.

Distinguer l'effet des tirs de la dynamique saisonnière des attaques

Le deuxième enjeu majeur de l'étude sera de dissocier la dynamique saisonnière des attaques, induite par les pratiques pastorales de transhumance, de celle qui est potentiellement modifiée par les tirs. En effet, le nombre d'attaques a naturellement tendance à diminuer à l'automne car les troupeaux quittent les unités de pâturage d'altitude pour retrouver les zones d'intersaison, puis les exploitations. Cette tendance naturelle à la baisse doit alors être dissociée de celle potentiellement provoquée par les tirs.

Penchons-nous par exemple sur le nombre moyen d'attaques dans un rayon de 2 km autour des prélèvements dérogatoires de loups depuis 2011, sur une période allant de 100 jours avant et après les prélèvements. Puis comparons ce nombre à celui qui est attendu si ces attaques étaient uniformément réparties dans l'espace et dans le temps autour des prélèvements.

Figure 3 **Identification des foyers de déprédation sur ovins (cercles bruns) pour la période s'étalant de mars 2016 à avril 2017 dans la région PACA et la partie est de la région Auvergne-Rhône-Alpes.**
Ces foyers sont constitués de surfaces pastorales (surfaces brunes) qui présentent ensemble significativement plus d'attaques que celles qui sont en dehors des foyers (surfaces jaunes) (d'après Grente *et al.*, en prép. ; données pastorales de l'IRSTEA, 2012).



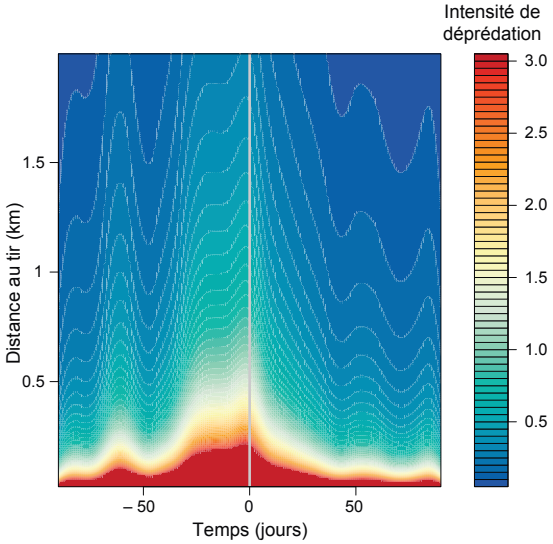


▲ *Prélèvement d'un loup dans les Alpes-de-Haute-Provence.*

De manière générale, que ce soit avant ou après le prélèvement, le nombre moyen d'attaques observé est plus grand que celui attendu lorsqu'on se situe à proximité immédiate du lieu du prélèvement (***figure 4***). Cependant, avant le prélèvement, on constate que cet écart s'étend aux troupeaux voisins au fur et à mesure

2. https://www.loupfrance.fr/entre-recherche-et-gestion-une-nouvelle-approche-pour-lanalyse-des-points-chauds-dattaques-de-loup-sur-ovins-en-france/

Figure 4 **Distribution de l'intensité relative de déprédation – de bleu (faible) à rouge (intense) – avant et après les dates des prélèvements dérogatoires de loups (prélèvements au temps 0 sur l'axe horizontal) et en fonction de la distance au site de tir (axe vertical) pour la période 2011-2018 en France.**
Des attaques uniformément réparties dans l'espace et dans le temps devraient donner une valeur d'intensité relative de 1 pour n'importe quel point donné. Au-delà de 1, il y a plus d'attaques observées qu'attendues.
N.B. : Pour une meilleure lisibilité, les intensités les plus fortes (4 % des valeurs, comprises entre 3,0 et 31,7) ont été ramenées à la valeur 3,0.



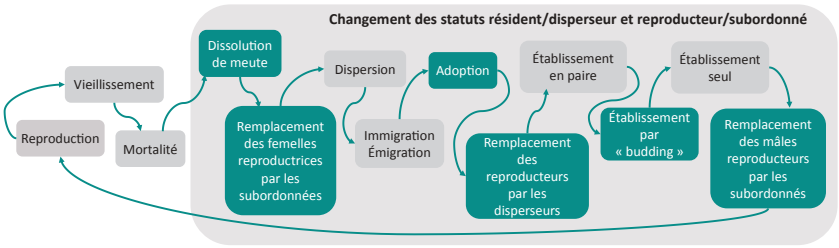
que la date du prélèvement se rapproche. Cela illustre que le tir est généralement appliqué après une augmentation locale de la pression de déprédation. Une fois le tir effectué, la situation s'inverse et le fort écart entre les nombres d'attaques observés et attendus devient de plus en plus restreint dans l'espace, pour ne plus concerner que la zone à proximité immédiate du prélèvement.

Cependant, si on pense observer ici un effet du tir, il pourrait s'agir en fait de la dynamique saisonnière des attaques concomitantes à la réalisation des tirs. En effet, les prélèvements ayant lieu essentiellement l'été, la diminution de l'espace concerné par la forte pression de déprédation que l'on observe après les prélèvements pourrait correspondre à celle qui survient naturellement à la fin de l'été, lorsque les troupeaux quittent les pâturages. La prise en compte des phénomènes saisonniers et hétérogènes de la dynamique des attaques dans le paysage pastoral est donc indispensable pour évaluer l'effet des tirs.

Une approche intégrée qui couple les trois composantes du système

Jusqu'à présent, nous étudiions directement l'effet des tirs sur les niveaux d'attaques constatés en réponse, sans prendre en compte explicitement les effets sur la population de loups ni les effets rétroactifs des niveaux d'attaques sur l'application du contrôle. Pour pallier cette lacune, nous avons commencé un travail de simulation du cycle entier de la ***figure 1***, en modélisant le fonctionnement d'une population de loups (***figure 5***). Cette approche est basée sur des modèles informatiques. Elle a pour but de donner un premier aperçu des effets potentiellement observables dans une population de loups à la suite des tirs, par exemple sur la reproduction, la stabilité des couples reproducteurs ou la dispersion.

Figure 5 **Schéma d'un modèle dit « individu-centré » simulant le cycle de vie des loups à travers différents processus représentés par les différents blocs.**
Les processus en bleu-vert ont été peu étudiés par les biologistes et sont explorés avec différents paramètres ou différents enchaînements dans l'article de Bauduin *et al.* (2020), d'où cette figure a été extraite.



Grâce aux données populationnelles récoltées par le réseau Loup-Lynx piloté par l'OFB[3], il est aussi possible de confronter ces modèles théoriques aux observations faites sur le terrain. Cette approche, complémentaire de la précédente, consistera à appliquer une nouvelle fois le protocole « avant/après les tirs », mais en intégrant les variables relatives à la composante de la population de loups.

Parce que ces informations sont complexes à récolter et à intégrer dans un modèle, l'étude se fera à une échelle locale, sur les quatre sites de Canjuers (83), de la Roya (06), de Bure (05) et de la Maurienne (73), sélectionnés en fonction des systèmes pastoraux, du nombre d'attaques, des prélèvements déjà réalisés dans le passé et des indices génétiques disponibles. Au vu du nombre limité de zones, cette analyse sera qualitative plutôt que quantitative et permettra d'étudier certains phénomènes observables localement, comme le remplacement des reproducteurs ou la dissolution des meutes, impossibles à observer à grande échelle.

Conclusion : l'utilisation des tirs létaux comme outil de protection des troupeaux est-elle efficace ?

La revue des articles qui se sont intéressés aux liens entre contrôle létal et déprédation a montré que le sujet fait

3. https://www.loupfrance.fr/wp-content/uploads/LE-SUIVI-GENETIQUE-DES-LOUPS-EN-2018_201903.pdf



▲ *Louveteau sur un site de rendez-vous dans les Hautes-Alpes.*

encore débat. Les études robustes sont à ce jour trop peu nombreuses. Face à l'augmentation des dommages aux troupeaux dus au loup, les gestionnaires français ont pourtant besoin d'évaluer l'efficacité de la politique de tir pour les réduire, et de savoir dans quelles mesures ce contrôle peut être appliqué sans mettre en jeu la viabilité de l'espèce en France.

S'il est tentant d'aborder la question en croisant directement le nombre de loups prélevés avec celui des attaques, cette approche corrélative est à éviter. En effet, le nombre d'attaques n'est pas uniquement lié au nombre de loups, mais aussi à une multitude d'autres facteurs. Il ne faut donc pas forcément s'attendre à une relation proportionnelle entre le nombre de loups prélevés et le nombre d'attaques. De plus, il est primordial de comprendre la distribution des attaques de loup en amont pour identifier leur dynamique naturelle en dehors de l'effet des tirs, mais aussi pour adopter des échelles d'analyse spatiales et temporelles appropriées.

En prenant en compte ces aspects, l'OFB et le CNRS ont défini un protocole d'analyse des effets des tirs dérogatoires sur les niveaux de déprédation due au loup en France, qui adopte la méthodologie la plus robuste possible à partir des données exploitables. Plusieurs approches complémentaires seront employées et mobiliseront des données à l'échelle nationale et à l'échelle locale.

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© P. Massit/OFB

▲ *Réalisation d'un constat de dommages sur ovin par un agent.*

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