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Pratiques, Prédateurs, Proies, Pullulation de Campagnols prairiaux et Biodiversité

par

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« Parfois, ce sont les gens dont on attend le moins qui font des choses auxquelles personne ne s'attendait » (Alan Turing – 1912-1954)

A un petit colibri...

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Résumé de la thèse

Dans le contexte des grands bouleversements socio-économiques, technologiques et environnementaux des révolutions agricoles, les zones de montagnes sont souvent considérées comme favorables à la biodiversité et à des pratiques agricoles respectueuses de l'environnement. Pourtant, ces territoires subissent une pression anthropique réelle via l'agriculture ou la sylviculture menant à une des questions fondamentales du siècle à venir sur l'altération des ressources naturelles par les activités anthropiques. Ces nouveaux systèmes agricoles ont entraîné l'émergence ou l'augmentation d'abondance d'espèces devenues des pestes agricoles. En raison des pertes de productions alimentaires, de la lutte chimique et des dégâts sur la faune non-cible, des réservoirs de zoonoses qu'ils représentent ou comme maillon essentiel des réseaux trophiques, les micro-mammifères et leurs pullulations représentent un domaine d'étude de première importance en écologie. Les politiques agricoles qui ont mené à une spécialisation des pratiques agricoles vers la production herbagère ont contribué à favoriser l'apparition des pullulations de campagnols prairiaux (campagnol terrestre et campagnol des champs) via l'augmentation de la production végétale et une homogénéisation du paysage agricole dans le Massif Jurassien et le Massif Central. Tandis que certains prédateurs comme les petits mustélidés se spécialisent dans la consommation de ces micro-mammifères. D'autres prédateurs, considérés comme généralistes, présentent une réponse fonctionnelle alimentaire en adaptant leur alimentation à la disponibilité de la ressource. Cette réponse fonctionnelle peut être à l'origine d'un report de prédation sur des proies alternatives aux micro-mammifères. Parmi toutes ces espèces, la petite faune chassable et patrimoniale représente à l'heure actuelle des enjeux de gestion et de conservation marqués.

Cette thèse a pour but de comparer deux zones géographiques (vallée alpine de la Haute-Romanche et Massif Jurassien) présentant un degré a priori différent de connaissances sur les systèmes de pullulations de campagnols prairiaux. Nous avons, au travers de ce travail, comparé le phénomène de pullulation observé en Haute-Romanche avec les connaissances actuelles du Massif Jurassien. Nous avons également, par l'analyse de données de monitoring à long terme et la mise en place d'expérimentations de terrain, essayé d'apporter des informations quant aux relations entre proies et prédateurs dans un système de pullulation de campagnol prairiaux en milieu tempéré. L'objectif est de tenter une comparaison tant que faire se peut entre les deux zones géographiques pour améliorer la gestion de ces écosystèmes.

Notre premier travail fut d'analyser les données récoltées entre 1998 et 2010 pour caractériser le fonctionnement spatio-temporel du campagnol terrestre en Haute-Romanche. Nous avons également confronté ces données à l'histoire agricole de la vallée entre 1810 et 2003 à l'échelle parcellaire. Dans un premier temps, nous avons constaté que le scénario historique agricole était similaire entre cette vallée de la Haute-Romanche et d'autres zones montagnardes européennes, avec une spécialisation sur la production herbagère et comme effet direct la disparition virtuelle des zones labourées, le cantonnement des zones de fauches dans les fonds de vallée et l'extension des zones de pâtures au reste des zones exploitées pour l'agriculture. En se basant sur ces données, nous avons pu mettre en évidence un lien corrélatif à l'échelle parcellaire entre l'occupation du sol actuelle et l'intensité de la pullulation du campagnol terrestre. Les zones pâturées ont présenté une amplitude de l'abondance en campagnol terrestre moins importante que les zones fauchées. L'occupation agricole actuelle étant directement dépendant de l'histoire agricole de la vallée, il apparaît vraisemblable que la spécialisation agricole vers la production herbagère dans cette vallée est, comme dans le Jura, à l'origine du développement de cet épisode de pullulation du campagnol terrestre.

Hormis la cyclicité du phénomène, qui reste à observer compte tenu de son aspect nouveau dans cette vallée, il existe de grandes similitudes avec les connaissances déjà acquises dans le Massif du Jura et en Auvergne. Ainsi, le développement de la pullulation à l'échelle parcellaire montre un processus étalé sur environ 5 années, avec au moins une période de pic puis un période de déclin et une période de faible abondance. D'un point de vue spatial, l'épisode de pullulation a montré une diffusion spatiale sous la forme d'une vague de colonisation canalisée par le relief, partant du Nord-Ouest puis remontant la vallée de la Romanche vers l'Est.

Dans le département du Doubs, après avoir tenu compte des tendances temporelles des données et de l'impact des traitements rodenticides sur notre zone d'étude, il apparaît qu'il existe une relation statistique négative entre l'abondance relative du lièvre d'Europe et celle du renard roux. Dans le même

temps, il existe également une relation positive entre l'abondance relative en lièvre d'Europe et celle du campagnol terrestre. Cette dernière peut être considérée comme une indication d'un potentiel report de prédation du renard roux sur le lièvre d'Europe. Néanmoins cette conclusion présente comme limite majeur, le fait de ne jamais inclure d'analyse de régime alimentaire du renard roux durant la même période, nécessaire pour renforcer l'hypothèse du report de prédation de cette espèce en particulier.

En travaillant sur la récolte de fèces de renard roux en Haute-Romanche, nous avons observé que, sur des parcours fixes, nous récoltions 4 à 5 fois plus de fèces en automne qu'en été et que, durant l'automne, les fèces étaient situées plus près des zones habitées. Concernant cette dernière observation, l'hypothèse proposée est la diminution ou la disparition de ressources alimentaires estivales et la dégradation des conditions climatiques en altitude forçant les renards roux à redescendre dans la vallée. Nous avons observé une forte occurrence d'insectes (et notamment d'orthoptères) dans le régime alimentaire du renard. Le campagnol terrestre et les campagnols du genre *Microtus* représente les micro-mammifères à l'occurrence la plus élevée dans les fèces de renard roux. Il semble que deux types de réponse alimentaire existent pour le renard roux dans notre système Alpin. Le premier est caractérisé par un comportement opportuniste du renard roux avec l'augmentation commune de certaines ressources alimentaires simplement en lien avec leur disponibilité saisonnière. Dans le même temps, lorsque l'abondance en campagnol terrestre diminue, l'occurrence d'autres items alimentaires augmente (fruits, méso ou macro-mammifères indéterminés, petits mammifères indéterminés et *Microtus* spp.). Il apparaît difficile de conclure à un report de prédation du renard roux sur les ressources alimentaires présentées ci-dessus. Toujours sur ces deux zones d'études, nous avons développé une approche expérimentale de la prédation par ajout et surveillance photographique d'une nouvelle « proie » (un leurre carné). La guildes observée des prédateurs est composée à 50% par des mammifères dominés par le renard roux et les animaux domestiques (chat et chien), à 40% par l'avifaune prédatrice dominée par les corvidés et dans 10% des cas par des prédateurs non identifiés. Ce dispositif nous a permis de constater une différence de vitesse de découverte du leurre carné en fonction du type de prédateur. Ainsi l'avifaune prédatrice découvre plus rapidement les leurres carnés que la plupart des prédateurs terrestres (le chat domestique présentant la même réponse que l'avifaune). La catégorisation en deux grandes typologies du paysage n'as pas permis de détecter d'effets de ce dernier sur la consommation du leurre. En utilisant une approche par analyses de données satellitaires, nous avons détecté un effet positif de l'augmentation de biomasse végétale sur la survie du leurre carné plaçant pour l'hypothèse d'un effet protecteur de la densité végétale. Néanmoins au vu de la faible part de variance expliquée par notre approche nous nous devons de rester prudents quant à cette observation.

La relation statistique positive entre l'abondance de certains prédateurs (renard roux, corneille noire, milan royal) et l'abondance en campagnol terrestre que nous observons nous permet d'envisager une réponse numérique partielle des prédateurs via une mobilité spatiale d'une zone de pullulation à une autre. Ce résultat s'affirme comme une information nouvelle dans des systèmes tempérés tels que nos zones de moyennes montagnes. Nous avons montré une relation positive entre la survie du leurre carné et l'abondance relative en campagnol terrestre. Ce résultat représente à nouveau une indication de l'existence potentielle d'un report de prédation dans notre expérimentation. La reconduction de ce dispositif dans la vallée alpine de la Haute-Romanche nous a apporté des observations similaires. Ceci nous a permis de renforcer nos conclusions concernant le faisceau d'indices plaçant en faveur d'un report de prédation et donc d'une réponse fonctionnelle des prédateurs. Cependant, la faible part de variance expliquée dans chacune de nos analyses dans les deux zones d'études met en question l'importance du phénomène en regard des autres sources de variations dans ce type de système à multiples ressources alimentaires et nombreuses interactions possibles.

En matière d'apport technique, ce constat amène donc à une réflexion à engager sur les moyens à mettre en œuvre pour limiter ce report de prédation potentiel sur des espèces dont le statut de conservation est déjà fragilisé. Un des résultats est la présence possible d'un effet positif qualifiable « d'effet refuge » de la biomasse végétale sur le temps de découverte des leurres carnés. La conclusion de cette thèse renforce l'idée qu'il faut attaquer la problématique globale du campagnol terrestre à la source en travaillant sur une rediversification paysagère. Concernant la prédation, les outils de régulation doivent être utilisés après concertation avec les différents organismes institutionnels en raison des questions économiques, éthiques et sanitaires qu'ils soulèvent. Pour renforcer les actions de terrain, la première des actions est le renforcement des systèmes d'observations de la faune sauvage sur le long terme et sur de larges échelles spatiales pour mesurer les effets potentiels des actions de gestion entreprises.

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Liste des communications relatives à la thèse

Publications

Halliez G, Renault F, Vannard E, Farny G, Lavorel S, Giraudoux P (2015) Historical agricultural changes and the expansion of a water vole population in an Alpine valley. *Agriculture, Ecosystems and Environment* 212 : 198-206.

Congrès internationaux

Halliez G, Renault F, Defrasne P, Becel C, Farny G, Longchamp P, Couval G, Truchetet D, Giraudoux P. Variation of predation pressure in a context of cyclic population outbreaks of grassland voles. 7th European Congress of Mammalogy – 17-21 August 2015 (oral communication), Stockholm, Sweden.

Congrès nationaux

Halliez G, Renault F, Vannard E, Greiner K, Lamarque P, Farny G, Lavorel S, Giraudoux P. L'histoire agricole, un outil pour mieux comprendre le fonctionnement spatio-temporel de pullulations actuelles de rongeurs. GdR 3359 MoDyS Rencontres Jeunes Chercheurs – 21-22 Novembre 2013, Frasnay, France.

Revue technique, presse et émission de radio

Quintaine T, Coeurdassier M, Halliez G, Truchetet D, Decors A (2014) Extension d'usage de la bromadiolone : les plaines de grandes cultures et les vergers sont maintenant concernés. Quelles conséquences pour la faune non cible ? *Lettre SAGIR* 180 : 5-7.

Est Républicain – 20/04/2013 – 800 saucisses dans la nature pour attirer les prédateurs.

Plaisir de la Chasse – Novembre 2013 – Des saucisses et des lièvres.

Chasseur Comtois – Décembre 2013 – Des saucisses et des lièvres.

Emission de radio « Radio Campus ». Table ronde sur la Zone Atelier Arc Jurassien.

Avant-propos

Cette thèse de doctorat a été réalisée dans le cadre d'une Convention Industrielle de Formation et Recherche (ANRT) avec un partenariat financier entre la Fédération Départementale des Chasseurs du Doubs et du Jura et le Parc National des Ecrins en collaboration principale avec l'UMR Chrono-Environnement (6249 CNRS/UBFC). Les différents partenaires ont pour objectif commun de mettre au point des techniques et des processus permettant de renforcer les systèmes d'observation de la faune existants et de développer les conditions conceptuelles, méthodologiques et humaines permettant d'évoluer vers un monitoring adaptatif (Lindenmayer et Likens, 2009) harmonisé des zones de montagne dont la dynamique des petits prédateurs et de leurs proies est en grande partie structurée par les espèces-clés que constituent les campagnols prairiaux. La démarche proposée était d'étudier de manière comparative et corrélative des écosystèmes montagnards de zones tempérées où se combinent forts enjeux agricoles, cynégétiques et de conservation.

Les travaux multidisciplinaires réalisés en Franche-Comté, depuis plus d'une trentaine d'années, et dans la Haute-Romanche, depuis plus d'une dizaine d'années, fournissent les bases de cette observation sur le long terme à plusieurs échelles et concernent l'évolution de l'agriculture, des paysages, et les populations de proies et de prédateurs. Ils impliquent, avec les chercheurs des 5 universités des UMR 6249 Chrono-environnement et 6049 ThéMA de l'Université de Bourgogne-Franche-Comté et de l'UMR 5553 LECA de l'Université Joseph Fourier de Grenoble, le personnel du Parc National des Ecrins, le Ministère de l'agriculture, la Fédération régionale de défense contre les ennemis des cultures de Franche-Comté, la Communauté de communes du Briançonnais, les Fédérations Départementales des Chasseurs du Doubs, du Jura et des Hautes-Alpes et l'Office national de la chasse et de la faune sauvage. Cette configuration unique, permettra de tester un certain nombre d'hypothèses sur l'effet des grandes fluctuations d'abondance de campagnols prairiaux sur les communautés de prédateurs et de proies alternatives.

Introduction générale

I - L'agriculture mondiale, son histoire et ses impacts sur l'environnement

I.1 - Quatre siècles de révolutions agricoles

L'histoire actuelle de l'agriculture mondiale se base sur quatre périodes distinctes de grands bouleversements sociaux, économiques, technologiques et environnementaux (Tableau 1). Bairoch (1989) situe ainsi la première révolution agricole en 1680/1700 en Angleterre et plus tardivement (1770/1810) dans les autres pays économiquement développés (Allen, 2000; Takata et al., 2009). Cette période est principalement caractérisée par la généralisation d'un système agricole à rotation de l'occupation du sol continue avec une forte diminution de la technique de la jachère. La deuxième révolution agricole, située autour de la seconde moitié du 19^{ème} siècle, est caractérisée par les débuts d'une mécanisation de certaines tâches agricoles dans un contexte de révolution industrielle (Hardeman et Jochemsen, 2012). La troisième révolution agricole, aussi appelée « révolution verte » est située après la seconde guerre mondiale et voit la généralisation, dans les pays développés, de la mécanisation, des intrants pétrochimiques et d'une intensification de la sélection génétique des organismes animaux comme végétaux notamment. Dans les pays du Sud économique, cette troisième révolution a eu lieu entre 1960 et 2000 : Asie, Afrique subsaharienne ou encore Amérique latine (Evenson et Gollin, 2003; Hardeman et Jochemsen, 2012). Bairoch (1989) introduisait le début de la quatrième révolution agricole que nous vivons à l'heure actuelle et qui concerne la technologie des organismes génétiquement modifiés et l'introduction de systèmes d'exploitations guidées par des technologies de l'information de haute performance.

Tableau 1 : Conséquences socio-économiques des révolutions agricoles.

Zone géographique	Conséquences	Référence bibliographique
	Temps nécessaire pour produire un milliard de tonnes de céréales en jusqu'en 1960 : 10 000 ans.	
Globale		Khush, 2001
	Temps nécessaire pour produire un milliard de tonnes de céréales entre 1960 et 2000 : 40 ans.	
Inde et Chine	Pour 1% d'augmentation de la production agricole, le nombre de personnes considérées comme pauvres diminue de 0,4% à 1,9%.	Thirtle et al., 2003
Etats-Unis d'Amérique et Canada	La production de blé a respectivement augmenté de 26 et 270 fois.	Olmstead et Rhode, 2011

Dans ce contexte de révolutions agricoles, les zones de montagnes sont souvent considérées comme des zones favorables à la biodiversité et à des pratiques agricoles respectueuses de l'environnement (Fjeldså et al., 1999). Pourtant, ces territoires subissent une pression anthropique réelle via l'agriculture ou la sylviculture (Chemini et Rizzoli, 2003; Tasser et al., 2009; Sitzia et al., 2010; Briner et al., 2012) qui est le plus souvent à l'origine des agro-écosystèmes semi-naturels ou artificiels actuels. Les différentes études sur les systèmes agricoles passés, en montagne, font état d'un système globalement identique sur tout le globe : de petits cheptels répartis sur des zones entièrement dédiées à la pâture et/ ou aux fauches alliés à des terres où est pratiquée une agriculture vivrière (Tiwari, 2000; Postigo et al., 2008; Niedrist et al., 2009; Nyssen et al., 2009; Negi et al., 2012). Ces études présentent donc à un système bâti, dans le passé, sur des pratiques agricoles et une occupation du sol diversifiées (Pôças et al., 2011). En Europe, au cours du 19^{ème} et du 20^{ème} siècle, les pratiques agricoles et l'occupation des sols ont subi une forte évolution (Le Roux et al., 2008) d'autant plus marquée dans les zones de montagnes. Ces changements sont caractérisés par deux phénomènes :

1 - Une déprise agricole avec pour conséquences l'abandon des terres agricoles dites à faible productivité et une augmentation des surfaces forestières (Dirnböck et al., 2003; López-i-Gelats et al., 2011; Tzanopoulos et al., 2011).

2 – Une évolution socio-économique tendant à une spécialisation des productions agricoles et à la dissociation spatiale et technologique de l'élevage et des cultures végétales (Le Roux et al., 2008). En plaine, cette spécialisation a été orientée vers la production de cultures céréalières, oléagineuses et légumineuses tandis qu'en zone de montagne l'agriculture s'est tournée vers la production fourragère d'herbe pour l'élevage bovin et/ou ovin (García-Martínez et al., 2011; Cocca et al., 2012) (Figure 1). Ces milieux montagnards sont ainsi connus pour être impactés par les activités anthropiques, à l'échelle du paysage, depuis de nombreux millénaires (Richard, 1997; Segard et al., 2003).

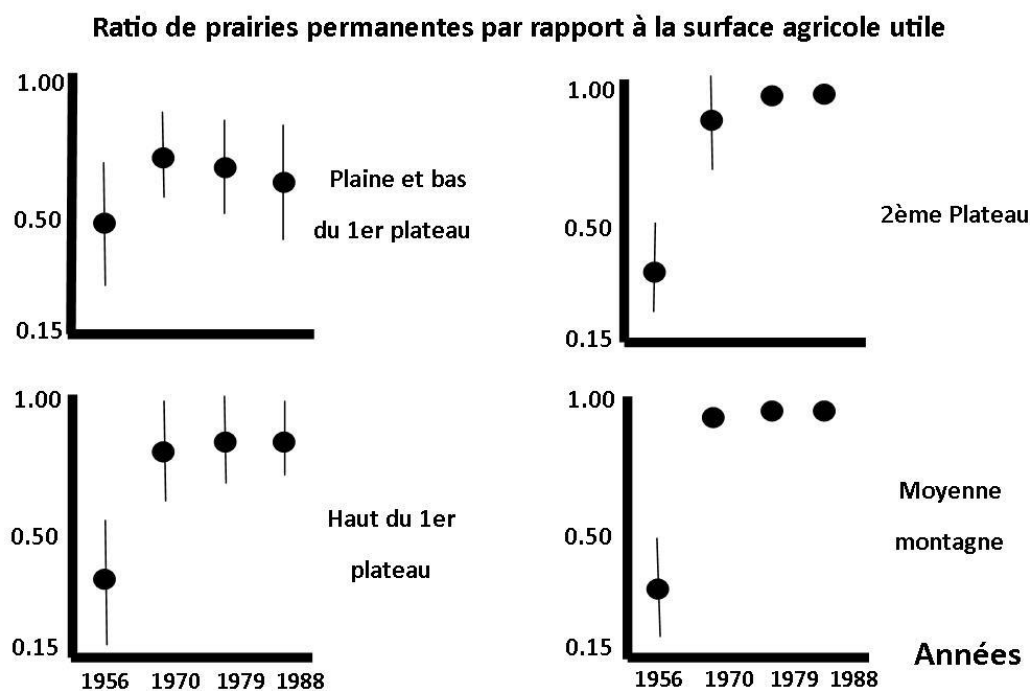


Figure 1 : Evolution du ratio de prairies permanentes par rapport à la surface agricole utile (SAU) dans le massif du Jura entre 1956 et 1988 (d'après Giraudoux et al., 1997).

Bien que les productions agricoles du Massif du Jura soient orientées de longue date vers l'élevage bovin à dominante laitière (Giraudoux et al., 1997), Boichard (1977) explique le caractère relativement récent de la spécialisation des pratiques agricoles vers la production fourragère avec notamment l'apparition d'openfields (zone présentant une occupation du sol quasi-uniforme sans habitats boisés) herbagers et

l'augmentation du cheptel bovin à partir des années 1950. Delattre et Giraudoux (2009) expliquent que ce phénomène de spécialisation agricole s'est accompagné d'une diminution du nombre de parcelles agricoles et du linéaire de haies et de murgers (murs en pierres sèches délimitant les parcelles agricoles) mais également d'une augmentation de la surface des parcelles utilisées (Tableau 2). Si l'on considère par exemple le département administratif du Jura et que l'on compare la composition de l'assolement agricole entre le début du 19^{ème} siècle (apparition du cadastre napoléonien) et l'assolement agricole récent (2012), on constate que les zones de production herbagère se sont relocalisées dans les zones de moyenne montagne tandis que les productions céréalières et assimilées se cantonnent désormais presque exclusivement aux zones de plaines.

Tableau 2: Spécialisation agricole herbagère dans le Massif Jurassien.

Elément paysager	Avant 1960-1970	Après 1960-1970	Référence bibliographique
Ratio de prairies permanentes dans la SAU du Massif Jurassien.	35%	Entre 80% et 100%	Giraudoux et al., 1997
Nombre de parcelles sur la commune de Sombacour (Doubs).	1980	429	Delattre et Giraudoux, 2009
Superficie moyenne des parcelles sur la commune de Sombacour (Doubs).	0,78 ha	2,78 ha	Delattre et Giraudoux, 2009
Evolution de la surface des haies sur la commune de Sombacour (Doubs).	Disparition de 21 691 m ²		Malfroy et al., 1981
Evolution de la surface des murgers sur la commune de Sombacour (Doubs).	Disparition de 2 292 m ²		Malfroy et al., 1981

Le massif Central n'échappe pas au glissement des pratiques agricoles d'une agriculture de montagne intégrant des cultures céréalières (seigle (*Secale cereale*)) vers des zones dévolues à une agriculture presque exclusivement tournée vers l'élevage et la production herbagère. Bordessoulle (2001) nous apprend ainsi qu'en 1922, les surfaces de cultures céréalières étaient encore de 14 000 hectares dans les Dores et 2000 hectares dans le canton de la Besse au début du 19^{ème} siècle. Dans le

Massif des Vosges, Koerner et al. (1999) font état d'une agriculture partagée entre agriculture céréalière et pâturages depuis au moins 2000 ans avec une apogée en termes de surfaces couvertes au cours du 18ème siècle. Au niveau de l'histoire agricole, Desfontaines et Raichon (1981) ont montré qu'au cours de la troisième révolution agricole (entre 1960 et 1980), quatre exploitations sur dix ont arrêté leur activité dans les Vosges du Sud. Dans les Pyrénées françaises, l'évolution de l'occupation des sols et les politiques agricoles ont mené à une augmentation des surfaces de chaque exploitation. Ainsi, dans les Midi-Pyrénées, la surface moyenne d'une exploitation agricole a augmenté de 28% entre 1970 et 1988 et de 44% entre 1988 et 2000 (Prosperi et al., 2010). En parallèle de cette augmentation des surfaces des exploitations, la surface des parcelles a également augmenté et les zones montagneuses ont observé une diminution de la diversité des cultures céréalières et une spécialisation vers la production herbagère (Prosperi et al., 2010). De la même manière, Rueff et al. (2012) ont montré, dans une étude sur cinq villages, que 95% des surfaces agricoles dites « privées » sont utilisées pour la production herbagère. Dans le même temps, entre 1955 et 2000, le nombre d'exploitations agricoles est passé de 120 exploitations (surface moyenne de 10 hectares) à 53 exploitations (surface moyenne de 16 hectares). Dans les Alpes, les premières preuves d'activité pastorale (défrichement et entretien) remontent à environ 2000 ans av. JC (Nakagawa et al., 2000; Segard et al., 2003) témoignant de l'ancienneté de ce mode de production dans les zones montagneuses. Néanmoins, les cultures céréalières et vivrières étaient également présentes de longue date. Le processus de spécialisation vers la production herbagère en Haute-Romanche (Alpes françaises) tend à débuter en 1830 (Tableau 3) avec l'apparition des premiers différents entre éleveurs et cultivateurs (Martin-Burle, 1991).

Tableau 3 : Les différentes étapes de la spécialisation agricole herbagère dans une vallée alpine (Haute-Romanche).

Date	Etapes	Référence bibliographique
1830	Apparition des premiers différents entre éleveurs et cultivateurs.	Martin-Burle, 1991
1836	1/6 ^{ème} des zones labourées ont déjà été converties en prairies.	Girel et al., 2010
1929	Surfaces de cultures passent de 177 ha à 85 ha.	Girel et al., 2010
1950	Surfaces de cultures passent de 85 ha à 15 ha.	Girel et al., 2010
1960-1985	Quasi-disparition des surfaces de cultures.	Girel et al., 2010

I.2 – Conséquences écologiques de l'évolution de l'agriculture mondiale

L'impact de la succession des différentes révolutions agricoles sur l'environnement est mesurable dans tous les compartiments de ce dernier. Une des questions fondamentales du siècle à venir est la réflexion sur l'altération des ressources naturelles par les activités anthropiques et notamment l'agriculture (Barbault et Chevassus-au-Louis, 2004). Parmi ces ressources, une des plus mise en avant à l'heure actuelle est la qualité des eaux superficielles (Cheng et al., 2002; Tiwari et Joshi, 2012). Les pratiques agricoles entraînent ainsi une augmentation des quantités de matière organique, des éléments traces métalliques, des produits d'origine pétrochimique dans l'eau tels que les pesticides (Thevenon et Poté, 2012). L'évolution des modes de production a également entraîné, par exemple, la baisse de la qualité des sols (Febles-González et al., 2011), leur érosion (Tiwari, 2000) ou encore l'homogénéisation des paysages (Loreau et al., 2001; Höbinger et al., 2012; Rohde et Hoffman, 2012).

II – Pestes agricoles et spécialisation agricole

II.1 – Définition d'une « peste agricole » et facteurs potentiels au phénomène de pullulation

L'intensification de l'agriculture est désormais reconnue comme une des plus grandes pressions anthropiques sur la biodiversité et les services écosystémiques qui lui sont associés (Hole et al., 2005). L'intensification des pratiques agricoles, l'homogénéisation du paysage et la diminution des systèmes de rotation ont entraîné l'émergence ou l'augmentation d'abondance d'espèces, autochtones ou allochtones, qui sont devenues des pestes agricoles. Au contraire, certaines espèces présentent une diminution inquiétante de leurs effectifs. Un certain nombre de micro-mammifères présentent la capacité à la fois d'atteindre un fort taux de croissance de leur population et une forte compétitivité inter-spécifique (Korpimäki et al., 2004). Ces caractéristiques peuvent, dans des agro ou sylvo-écosystèmes déstabilisés, engendrer des pullulations. Le phénomène de pullulation dans le temps d'une espèce animale est défini comme étant la variation statistiquement significative de son abondance entre une phase dite de basse abondance à une phase dite de forte abondance (Campbell, 1995). Ces pullulations peuvent être de nature temporelle différente à savoir absente, éruptive, épisodique ou cyclique (Figure 2) (Delattre et al., 1992).

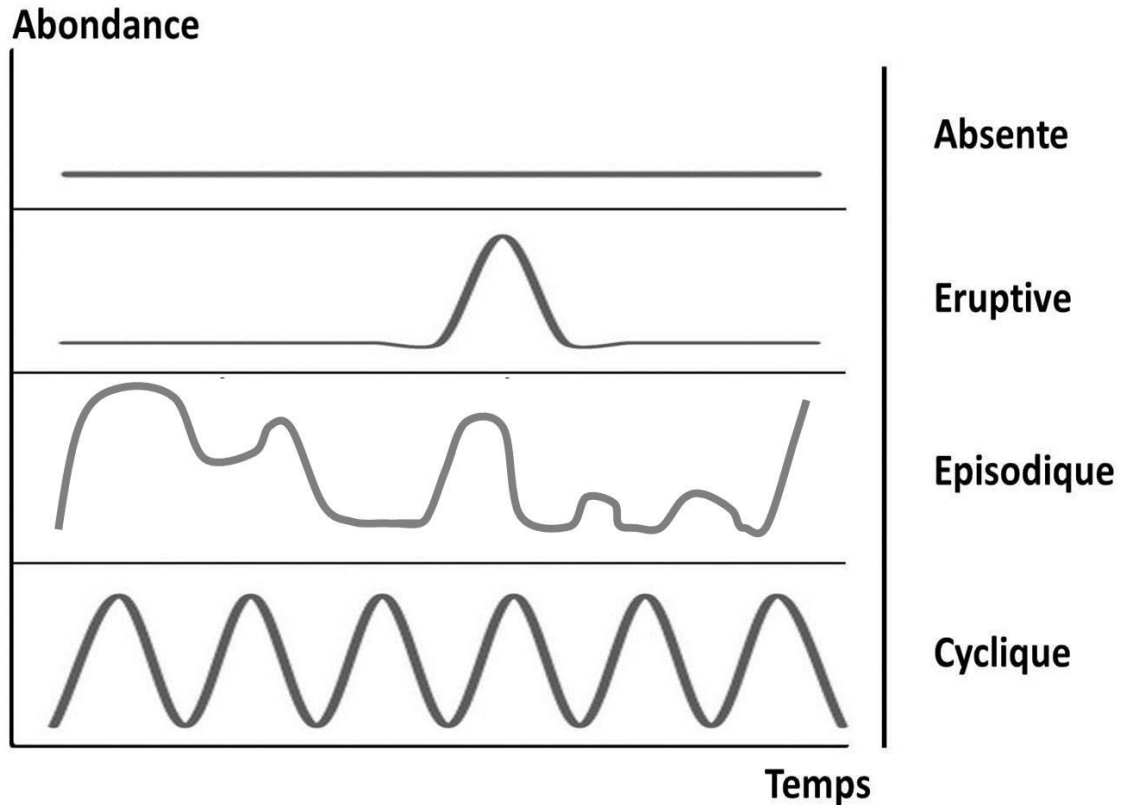


Figure 2 : Les différents types théoriques de pullulations.

Dans le cas des micro-mammifères, la variation d'abondance dans le temps d'une population va principalement dépendre de son taux d'accroissement (Krebs, 2013) et plus particulièrement des facteurs intrinsèques (capacité à se reproduire (Hansson et Henttonen, 1985), survie des individus, productivité en jeunes (Stenseth et al., 1985) par exemple) et extrinsèques (prédation (Erlinge et al., 1983), parasitisme, conditions météorologiques (White, 2011), disponibilité alimentaire (Jareño et al., 2015)) à la population et des relations complexes qui peuvent exister entre ces différents facteurs. Butet et Spitz (2001) ou Krebs (2013) expliquent ainsi, qu'en plus de la prise en compte de tous ces facteurs potentiels, la mise en évidence de la nature temporelle de la dynamique d'une population de micro-mammifère va également dépendre de la méthode d'observation du phénomène (population « fermée » ou non, méthode de collecte des données), de l'échelle spatiale choisie (une partie d'une population de micro-mammifères peut simultanément pulluler à un endroit donné et ne pas pulluler dans un autre lieu géographique pourtant potentiellement connectés) ou encore de l'échelle temporelle choisie (mise en évidence d'une variation saisonnière pour

quelques mois de suivis, d'une dynamique cyclique pour quelques années, et d'une remise en cause de la régularité d'une dynamique cyclique pour des décennies de suivis). Il existe aussi une définition plus socio-économique de la pullulation qui ne correspond pas forcément à une variation significative de l'abondance mais plus à un niveau d'abondance toléré par l'homme (par exemple les agriculteurs) (Delattre et Giraudoux, 2009). Ce phénomène temporel de pullulation peut s'accompagner d'un phénomène de propagation spatiale de la pullulation soit de manière isolée soit sous forme de vague voyageuse. Dans ce dernier cas, l'organisation spatiale des différents sites présentant un phénomène de pullulation cyclique va s'organiser selon un gradient géographique déterminé avec une vitesse de propagation déterminé par le rapport entre la surface occupée par chaque groupe d'individus et la durée de leur cycle de pullulation (figure 3) (Sherratt, 2001; Sherratt et Smith, 2008; Berthier et al., 2013).

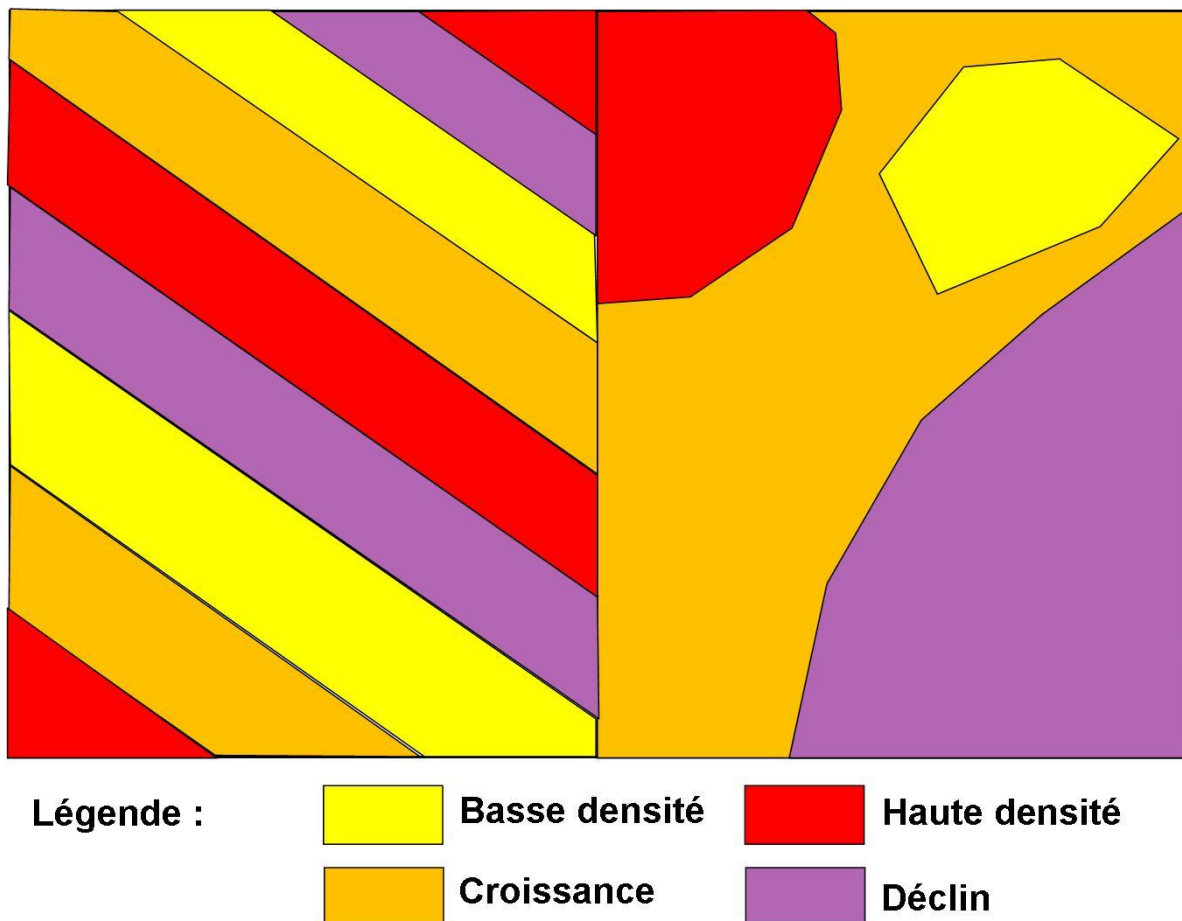
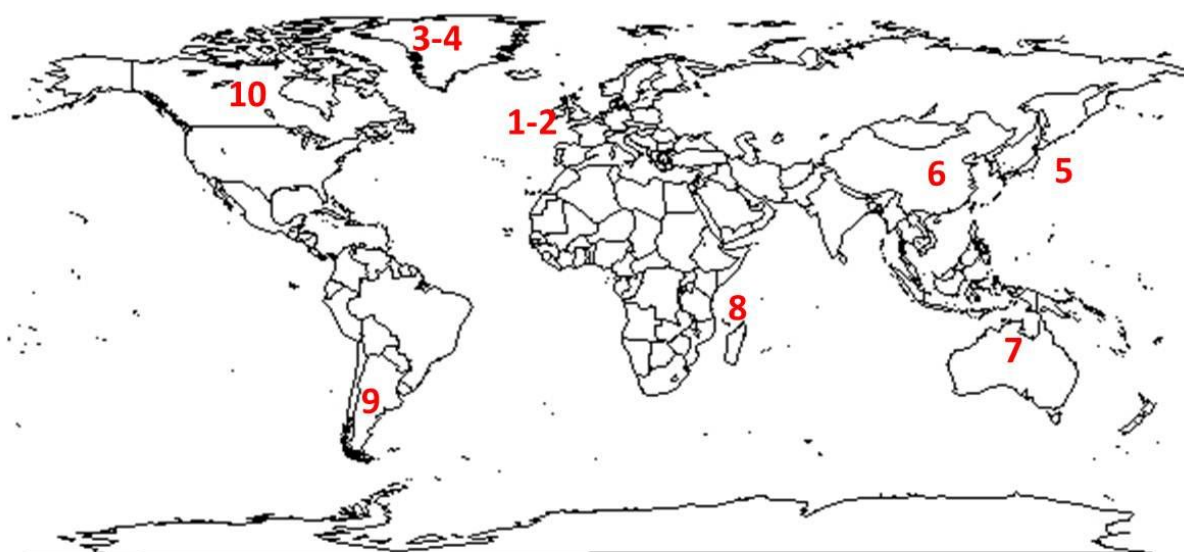


Figure 3 : Représentation d'un fonctionnement en vague voyageuse d'une population cyclique (gauche) et d'une population cyclique sans organisation en vague voyageuse (droite) d'après Sherratt et Smith (2008).

Les pullulations de micro-mammifères peuvent également être liées aux conditions climatiques telles que les précipitations (Stenseth et al., 2003; Zhang et al., 2003; Ims et al., 2011). Ainsi, White (2011) a montré que dans les zones sub-Arctique, l'altération de la cyclicité des populations de campagnols agreste (*Microtus agrestis*), de campagnol roussâtre (*Clethrionomys glareolus*) et de campagnol de Sundevall (*Clethrionomys rufocanus*) pouvait être reliée à une augmentation des températures hivernales et donc à des périodes d'enneigement plus courtes. L'hypothèse émise par cet auteur est que ces périodes d'enneigement plus courtes et des températures plus clémentes plus fréquentes permettraient aux végétaux des floraisons et des grenaisons plus régulières d'années en années et donc fourniraient une ressource alimentaire plus stable dans le temps pour les jeunes campagnols. La survie des jeunes campagnols en serait plus stable et pourrait expliquer l'altération de la cyclicité de ces espèces. Globalement, il apparaît que le cas de pullulations de micro-mammifères en relation avec des données climatiques sont connus mondialement dans la littérature scientifique (Figure 4).



- | | |
|--------------------------------|---------------------------|
| 1 – Jareño et al., 2015 | 6 – Zhang et al., 2003 |
| 2 – Cornulier et al., 2013 | 7 – Krebs et al., 2004 |
| 3 – Gilg et al., 2009 | 8 – Stenseth et al., 2003 |
| 4 – Gilg et al., 2012 | 9 – Andreo et al., 2009 |
| 5 – Hansson et Henttonen, 1998 | 10 – Hone et al., 2011 |

Figure 4 : Localisation d'exemples de lien entre pullulations de micro-mammifères et conditions climatiques dans le monde.

Dans les milieux semi-arides, il existe une relation positive entre le niveau des précipitations et l'existence de pullulation de rongeurs (Lima et al., 2002; Krebs et al., 2004). L'hypothèse d'un lien complexe entre précipitations, ressource alimentaire et survie des rongeurs est avancée, même si Krebs et al. (2004) affirment que ce lien est trop complexe pour être encore totalement expliqué.

L'intensification et/ou la spécialisation agricole peuvent favoriser les populations de micro-mammifères en :

- 1 - augmentant la disponibilité en ressources alimentaires (Parshad, 1999),
- 2 - en modifiant la composition et la structure paysagère ce qui peut modifier l'abondance ou la composition des communautés de prédateurs ou modifier les barrières naturelles qui, en modulant la dispersion individuelle, jouent un rôle important dans la régulation des populations des micro-mammifères (Michel et al., 2006, 2007; Falk et al., 2011; Fernex et al., 2011).

Ainsi, la plupart des études à travers le globe montrent qu'un paysage et une occupation du sol fragmentés et diversifiés sont favorables à la diversité de la communauté de micro-mammifères (Sutherland et al., 2014) tandis que les zones agricoles présentant des paysages et une occupation du sol homogènes présentent une diversité taxonomique très faible mais de gros effectifs (Monadjem, 1999; Arlettaz et al., 2010). Au niveau européen, un des derniers exemples récents de l'impact de la spécialisation agricole sur le développement de pullulations cycliques de micro-mammifères est l'apparition du campagnol des champs (*Microtus arvalis*) puis sa pullulation chronique dans le nord de l'Espagne. Ce dernier était absent dans cette zone géographique dans les années 1960. Le passage d'une agriculture en zone aride à une agriculture irriguée à partir des années 1960 a permis l'accroissement de la biomasse végétale produite et sa colonisation par le campagnol des champs. Il s'en est suivi une pullulation chronique depuis 1967 (première pullulation observée) (Luque-Larena et al., 2013; Jareño et al., 2014, 2015). Ce phénomène récent est historiquement général en Europe tempérée : les politiques agricoles qui ont mené à une spécialisation des pratiques agricoles vers la production herbagère ont contribué à favoriser l'apparition des pullulations de campagnols prairiaux (Delattre et al., 1992,

Giraudoux et al., 1997, Fichet-Calvet et al., 2000, etc.). La première raison est l'augmentation de la capacité du milieu à produire de la biomasse végétale servant à nourrir les campagnols par l'intensification de pratiques telles que la fertilisation ou la fauche (de Montard, 1991; Morilhat et al., 2007). Les campagnols prairiaux, affectionnant les dicotylédones (par exemple le trèfle blanc (*Trifolium repens*)) et dans une moindre mesure les graminées (Quéré et Le Louarn, 2011), peuvent être favorisés d'un point de vue alimentaire par la dominance de ce type de végétaux dans un contexte de prairies fauchées et amendées. Ainsi, Newton et al. (2012), dans un suivi de 88 sites européens de prairies calcicoles soumises à une augmentation de la fertilisation sur 70 ans montrent que le trèfle blanc, espèce fortement dépendante de la disponibilité en azote (Varin et al., 2009), s'est accru de façon significative en Europe. Un autre impact de l'évolution de ces pratiques, associé aux remembrements agricoles, est une augmentation des surfaces toujours en herbe qui sont connues pour être un habitat favorable pour les campagnols prairiaux (Giraudoux et al., 1997; Briner et al., 2005) et donc un facteur prépondérant dans le démarrage des pullulations dans le Massif Jurassien (Giraudoux et al., 1997; Morilhat et al., 2007, 2008).

II.2 – Exemples de conséquences de pullulations de micro-mammifères

L'étude des pullulations de ces micro-mammifères revêt un intérêt pluri-disciplinaire. Parmi les domaines considérés, on peut citer l'économie agricole en raison des pertes de production alimentaires imputées dans de nombreux endroits de la planète (Parshad, 1999; Curtis et al., 2002; Zhang et al., 2003; D'Andrea et al., 2007; Sluydts et al., 2009; Singleton et al., 2010; Fraschina et al., 2012) (Figure 5). En effet, si les dégâts agricoles liés aux pullulations de micro-mammifères est un processus qui revêt une importance économique au niveau mondial, il revêt parfois d'une importance vitale pour nombre de populations humaines des pays pauvres et émergents (Mwanjabe et al., 2002; Singleton, 2003; Singleton et al., 2005b; Meerburg et al., 2009; Jacob et al., 2010; Monadjem et al., 2011).

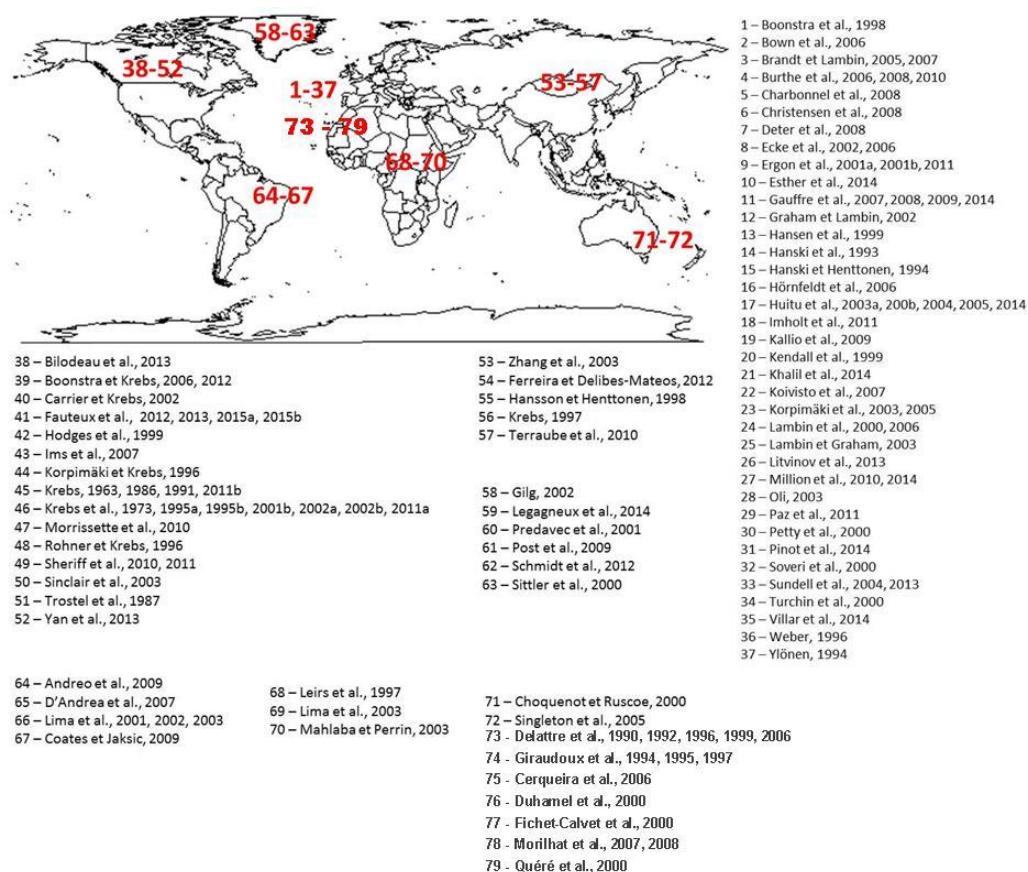
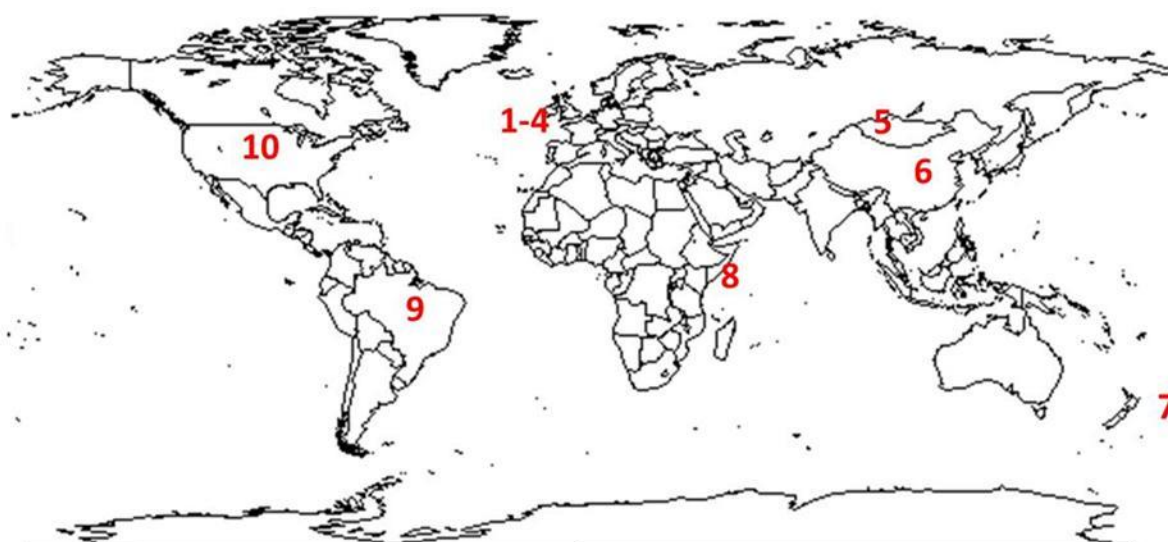


Figure 5 : Localisation d'exemples de pullulations de micro-mammifères dans le monde.

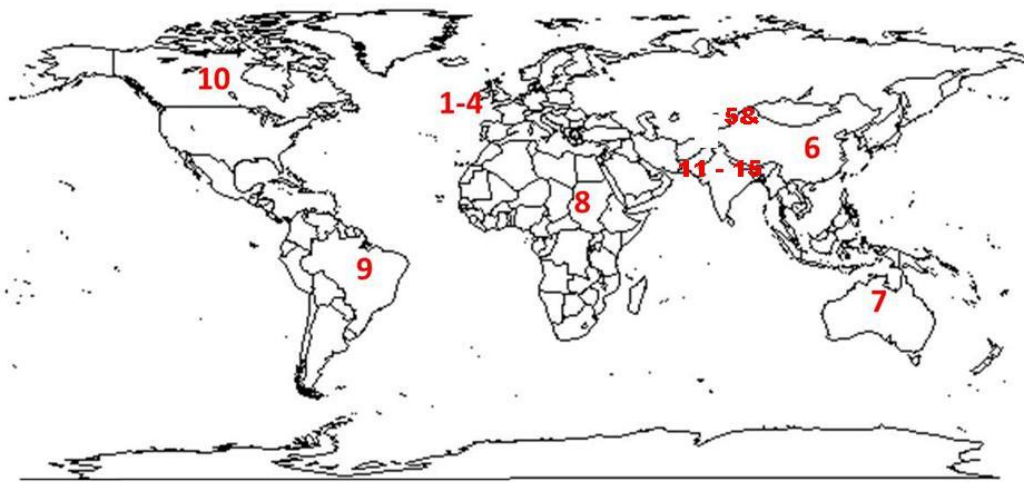
Ces « pestes agricoles » ont un coût économique et environnemental directement lié au contrôle de ces dernières (Schreinemachers et Tipraqsa, 2012). Le contrôle des pullulations de rongeurs via l'utilisation de rodenticides pose la question de l'impact de ces traitements sur la faune non-cible et les populations humaines lors des transferts de contaminant par consommation de proies empoisonnées (Zhang et al., 2003; Sage et al., 2008; Berny et al., 2010; Coeurdassier et al., 2012; Gabriel et al., 2012; Jacquot et al., 2013; Coeurdassier et al., 2014; Montaz et al., 2014; López-Perea et al., 2015) (Figure 6).



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|-------------------------------|--------------------------------|
| 1 – Mougéot et al., 2011 | 6 – Zhang et al., 2003 |
| 2 – Tosh et al., 2011 | 7 – Parkes et al., 2011 |
| 3 – Christensen et al., 2012 | 8 – Gratz et Arata, 1975 |
| 4 – Coeurdassier et al., 2012 | 9 – Kaudeinen et Rampaud, 1986 |
| 5 – Winters et al., 2010 | 10 – VanderWerf, 2001 |

Figure 6 : Localisation d'exemples d'utilisation de rodenticides anticoagulants en lien avec des pullulations de micro-mammifères dans le monde.

Enfin, la capacité des micro-mammifères à pulluler en font des espèces clés dans le fonctionnement des agro-écosystèmes en tant que réservoir de zoonoses (Boué et al., 2010; Wang et al., 2010; Decors et al., 2011; Said-Ali et al., 2013; Guerra et al., 2014; Mayer-Scholl et al., 2014) (Figure 7) ou comme maillon essentiel des réseaux trophiques, notamment comme ressource alimentaire de la communauté de prédateurs (Hanski et al., 2001; Ekerholm et al., 2004; Korpimäki et al., 2004).



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|-------------------------------|-----------------------------|-------------------------|
| 1 – Luque-Larena et al., 2013 | 6 – Marston et al., 2014 | 11 - Wang et al., 2011 |
| 2 – Knapp et al., 2014 | 7 – Slack et al., 2006 | 12 - Zhang et al., 2009 |
| 3 – Liccioli et al., 2015 | 8 – Taylor et al., 2008 | 13 - Zhang et al., 2010 |
| 4 – Hegglin et al., 2015 | 9 – Enria et Pinheiro, 2000 | 14 - Yin et al., 2008 |
| 5 – Giraudoux et al., 2013 | 10 – Liccioli et al., 2014 | 15 - Yin et al., 2011 |

Figure 7 : Localisation d'exemples de problèmes sanitaires conséquents à la présence de zoonoses en lien avec des pullulations de micro-mammifères dans le monde.

III - Cyclicité des populations de micro-mammifères et communauté de prédateurs

Les études des relations entre l'évolution spatio-temporelle des densités de micro-mammifères et les communautés de prédateurs représentent un domaine de recherche important pour la communauté scientifique (Lidicker, 2000; Vaniscotte et al., 2009; Ims et al., 2011; Lehikoinen et al., 2011). En effet, la compréhension du rôle réel de l'importance de ces proies souvent les plus disponibles dans les systèmes nordiques (Hanski et al., 2001; Ekerholm et al., 2004; Gilg et al., 2006; Bilodeau et al., 2014) sur les réseaux trophiques est fondamentale notamment pour quantifier leurs dysfonctionnements naturels ou anthropiques (Gilg et al., 2003; Ekerholm et al., 2004).

Que l'on se place dans des systèmes américains avec le chien de prairie (*Cynomys* spp.), européens avec les campagnols ou asiatiques avec les Pikas (*Ochotonidae*), la biomasse produite représente une ressource alimentaire essentielle pour les communautés de prédateurs sédentaires ou migrants (Löfgren et al., 1986; Korpimäki, 1989; Hörnfeldt, 2004; Díaz-Ruiz et al., 2010; Lanszki et Heltai, 2011;

Angerbjörn et al., 2013; Fernandez-De-Simon et al., 2014). C'est le cas aussi des campagnols prairiaux dans les montagnes françaises (Tableau 4).

Tableau 4 : Prédateurs et principaux consommateurs de campagnols prairiaux dans les zones de moyennes et hautes montagnes en France.

Espèces prédatrices et consommatrices	Référence
Renard roux (<i>Vulpes vulpes</i>)	Dell'Arte et al., 2007
Chat forestier (<i>Felis silvestris</i>)	Quéré et Le Louarn, 2011
Chat domestique (<i>Felis catus</i>)	Tschanz et al., 2011
Fouine (<i>Martes foina</i>)	Lachat Feller, 1993
Martre des pins (<i>Martes martes</i>)	Russell et Storch, 2004
Hermine (<i>Mustela erminea</i>)	Delattre et Giraudoux, 2009
Belette d'Europe (<i>Mustela nivalis</i>)	Savouré-Soubelet et al., 2012
Putois d'Europe (<i>Mustela putorius</i>)	Weber et al., 2002
Milan royal (<i>Milvus milvus</i>)	Coeurdassier et al., 2012
Buse variable (<i>Buteo buteo</i>)	Berny et al., 1997
Faucon crécerelle (<i>Falco tinnunculus</i>)	Schmidt et al., 2002
Busard Saint-Martin (<i>Circus cyaneus</i>)	Quéré et Le Louarn, 2011
Hibou Grand-Duc (<i>Bubo bubo</i>)	Bayle et Schauls, 2011
Effraie des clochers (<i>Tyto alba</i>)	Bernard et al., 2010
Hibou moyen-duc (<i>Asio otus</i>)	Quéré et le Louarn, 2011
Chouette hulotte (<i>Strix aluco</i>)	Roulin et al., 2008
Corneille noire (<i>Corvus corone corone</i>)	Quéré et Le louarn, 2011
Héron cendré (<i>Ardea cinerea</i>)	Quéré et Le Louarn, 2011
Pie-grièche grise (<i>Lanius excubitor</i>)	Lefranc et Paul, 2011
Vipère aspic (<i>Vipera aspis</i>)	Quéré et Le Louarn, 2011

Ainsi, Coeurdassier et al. (2012) soulignent le fait que les pics de pullulations de campagnol prairiaux représentent pour une espèce opportuniste comme le milan royal (*Milvus milvus*), une source de nourriture importante lors des migrations. En Espagne, le déclin de deux espèces de prédateurs menacées (le lynx ibérique (*Lynx pardinus*) et l'aigle ibérique (*Aquila adalberti*)) a également pu être lié au déclin du lapin de garenne (*Oryctolagus cuniculus*) (Delibes-Mateos et al., 2007, 2008, 2009a, 2009b, 2014; Fernandez-De-Simon et al., 2011a, 2011b). De même, l'évolution démographique de la population de Busard Saint-Martin des îles Orkney en Ecosse a été liée aux fluctuations de la disponibilité en campagnols prairiaux (Amar et al., 2003). Enfin, il a été démontré que les populations de putois à pieds noirs (*Mustela nigripes*) ne se maintiennent que dans les zones où la densité en chiens de prairie restent élevées (Delibes-Mateos et al., 2008).

On reconnaît généralement deux types de réponse des prédateurs à la variation d'abondance d'une ressource alimentaire. La première est la réponse fonctionnelle définie comme le taux de nourriture consommée par un prédateur en fonction de l'abondance en ressource alimentaire. Holling (1966) subdivise la réponse fonctionnelle en trois types (Figure 8) :

- La réponse de Holling type I est définie par un accroissement linéaire de la quantité de ressource alimentaire consommée par un prédateur en lien avec l'accroissement de sa disponibilité jusqu'à une quantité limite à partir de laquelle la consommation par le prédateur présente un aspect de plateau.
- La réponse de Holling type II, la présence d'une limitation du prédateur dans sa capacité à consommer va entraîner une phase de ralentissement dans la consommation d'une ressource alimentaire induisant une relation non-linéaire entre le taux de consommation et l'abondance de la ressource par opposition à la linéarité de la réponse de type I.
- La réponse de Holling de type III présente, à basse abondance en ressource alimentaire, une relation quasi-exponentielle entre la quantité de nourriture consommée par un prédateur et l'abondance de cette dernière.
- Ce phénomène est souvent présenté comme dépendant d'une part d'un temps de latence du prédateur pour une ressource alimentaire ou par un phénomène de report de prédation. Le report de prédation d'un prédateur implique la présence de plusieurs ressources alimentaires potentielles. Le prédateur va

alors ajuster son régime alimentaire en fonction des fluctuations d'abondances propres à chacune des ressources alimentaires disponibles.

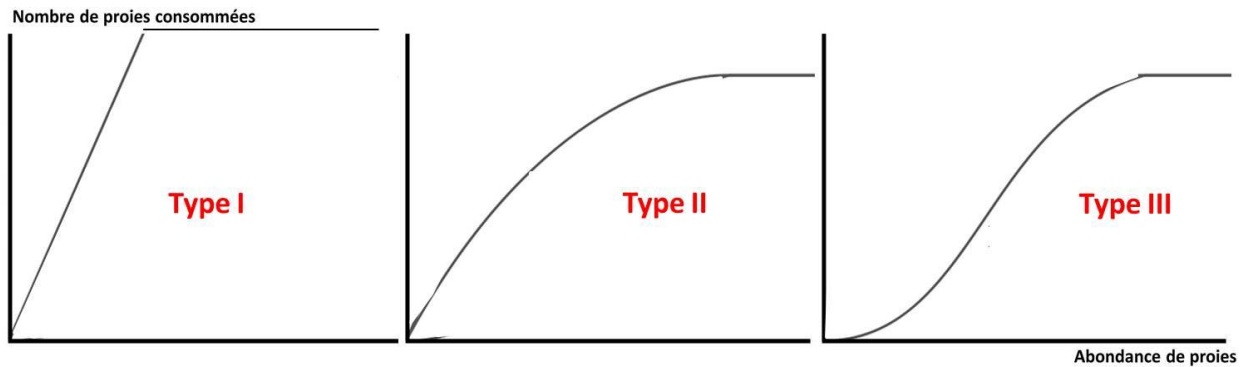


Figure 8 : Représentation théorique des trois types de réponses fonctionnelles d'un prédateur décrites par Holling (1966).

La réponse numérique (Figure 9) est définie comme un changement d'abondance d'un prédateur en fonction du changement d'abondance de sa ressource alimentaire. La réponse numérique peut être définie par deux types de mécanismes (non exclusifs) :

- une variation du succès de reproduction du prédateur,
- une agrégation spatiale des prédateurs par des phénomènes d'immigration et émigration.

**Abondance
du prédateur**

**Abondance
de la ressource**

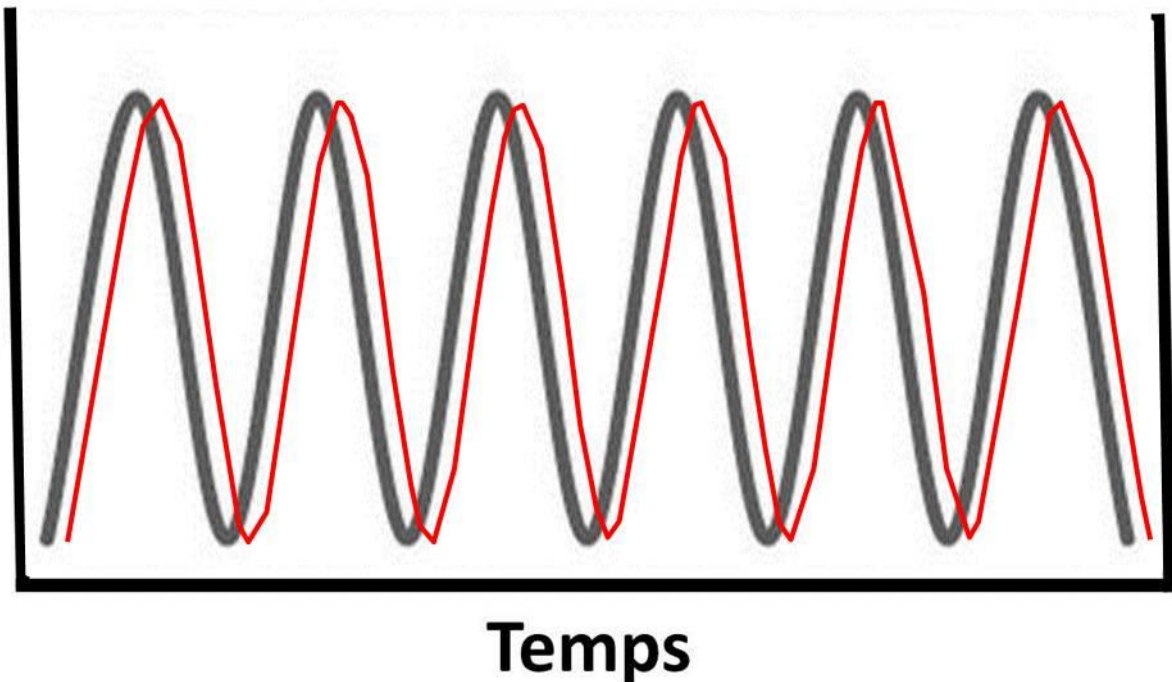


Figure 9 : Représentation théorique de la réponse numérique d'un prédateur (en rouge) par rapport aux fluctuations de sa proie (en gris).

Ainsi, certains prédateurs (e.g. hermine (*Mustela erminea*), belette d'Europe (*Mustela nivalis*)), se spécialisent dans la consommation de ces micro-mammifères. Gilg et al. (2006) ont montré par une analyse du régime alimentaire de l'hermine sur 15 années que la part de biomasse sèche des fèces était composé au minimum de 98,5% de lemmings à collerette (*Dicrostonyx groenlandicus*). D'autres prédateurs, comme le renard roux (*Vulpes vulpes*) ou la martre des Pins (*Martes martes*), sont capables d'adapter leur régime alimentaire à la nature de la ressource (Russell et Storch, 2004; Dell'Arte et al., 2007; Sidorovich et al., 2009). Pour ces deux espèces, dans un contexte méditerranéen, Padial et al. (2002) ont montré que le régime alimentaire présentait une variation saisonnière dans un premier temps et que chacune des espèces basait son régime alimentaire sur quelques taxons mais était capable d'adapter son régime alimentaire en fonction de la disponibilité en ressources alimentaires. Ceci est caractérisé par le fait que dans cette étude (Padial et al., 2002), la consommation de fruits par les deux espèces était fonction de la disponibilité et de

la saisonnalité. Dans leur étude mettant en relation l'évolution du régime alimentaire de différents prédateurs considérés comme généralistes et les fluctuations d'abondance de micro-mammifères, Dupuy et al. (2009) ont démontré que lors du passage d'une phase de haute densité à une phase de basse densité la fouine, la martre, le renard roux et le chat domestique présentait une réponse fonctionnelle. Néanmoins ces auteurs expliquent que cette réponse est plus lente à se mettre en place chez le renard roux et le chat domestique. Néanmoins, il est à noter que dans des systèmes où les ressources alimentaires alternatives sont plus rares, le renard roux peut présenter un comportement spécialisé sur la consommation de micro-mammifères (Andersson et Erlinge, 1977). Les prédateurs considérés comme généralistes, comme le renard roux ou la martre des Pins, présentent une réponse fonctionnelle alimentaire. La réponse fonctionnelle de certains prédateurs généralistes vis-à-vis des pullulations de campagnols prairiaux peut, elle, être à l'origine d'un report de prédation d'une partie de la communauté de prédateurs sur des proies alternatives (Korpimäki and Krebs, 1996; O'Donoghue et al., 1998; Gilg et al., 2006; Panzacchi et al., 2008; Morrissette et al., 2010).

L'existence de ces deux types de réponse alimentaire peut être complétée chez certaines espèces de prédateurs par une réponse numérique au niveau de la reproduction. Ainsi, la dynamique des populations des prédateurs spécialistes peut alors être régulée par l'abondance de proies. Hellstedt et al. (2006) ont montré que l'abondance de l'hermine et la belette d'Europe, selon la méthode des « Wildlife triangle census » (Pellikka et al., 2005) était fonction de la disponibilité en campagnols. Ce constat est partagé par de nombreuses études dans ces systèmes sub-Arctiques et tempérés (Debrot, 1983; Hanski et al., 2001; Ekerholm et al., 2004; Gilg et al., 2006). Dans un contexte de pullulations cycliques de lemmings et la présence de quatre espèces prédatrices, Gilg et al. (2003) ont montré que seule l'hermine présentait une réponse numérique en termes d'abondance avec un an de retard sur les pics de pullulation. Les auteurs montrent également dans les systèmes sub-arctiques que la nature de la réponse des prédateurs a également un impact direct sur les fluctuations d'abondance des micro-mammifères. Ainsi, il est attesté que la spécialisation alimentaire de prédateurs comme l'hermine entretiennent la cyclicité marquée des populations de micro-mammifères (Gilg et al., 2006). Ce processus serait expliqué par le fait que la fluctuation des densités de micro-mammifères, et donc de la ressource

alimentaire, impacte directement le nombre d'individus prédateurs sur une zone spatiale définie. Ainsi, les densités d'hermine augmenteraient en fonction de la phase de croissance et de pullulation des micro-mammifères entraînant un déclin marqué de la densité de ces derniers. Ce déclin diminuerait donc la ressource alimentaire des prédateurs spécialistes qui auraient de ce fait tendance à se raréfier rendant possible une nouvelle croissance des populations de micro-mammifères. Dans le cas de l'île de Wrangel (Russie) caractérisée par l'absence de mustélidés, Menyushina et al. (2012) tempèrent cette hypothèse en indiquant que les populations de lemmings présentent tout de même des fluctuations cycliques de leur abondance avec simplement une fréquence plus importante des phases d'abondance intermédiaire.

III.1 - Pullulations de campagnols prairiaux et report de prédation

L'étude des réseaux trophiques permet de dire que dans les agro-écosystèmes et les sylvo-écosystèmes la relation unique d'une espèce prédatrice avec une espèce proie est considérée comme trop simpliste. Il est admis (Holt et Huxel, 2007; Blanco-Aguilar et al., 2012) que, mis à part dans des écosystèmes très particuliers et extrêmement simples au niveau du fonctionnement trophique, les réseaux trophiques sont composés d'une communauté d'espèces pouvant être considérées comme proies *stricto sensu*, comme proies ou comme prédateurs ou comme prédateurs *stricto sensu*. Les populations qui composent ces communautés entretiennent des relations complexes entre elles. Dans le cas de systèmes gouvernés par l'abondance d'une proie qualifiée de peste, le report de prédation des prédateurs généralistes sur d'autres espèces de proies qualifiées de proies non-pestes a été prouvé et permet le maintien des densités de prédateurs (Holt, 1977; Hardwood et Obrycki, 2005; Koss et Snyder, 2005).

Un certain nombre d'études apportent des informations quand à ces possibles phénomènes de report de prédation dans un contexte de pullulations cycliques de micro-mammifères (Bêty et al., 2001; Hansson, 2002; Kjellander et Nordström, 2003; Moss et al., 2010; Tornberg et al., 2012). Par exemple, en Europe, parmi les espèces considérées comme généralistes, deux espèces sont connues pour exercer un report de prédation sur des proies alternatives aux campagnols prairiaux : le renard roux et la martre des pins (Marchesi et al., 1989).

Parmi les prédateurs des campagnols prairiaux cités dans le Tableau 4, un certain nombre sont capables d'utiliser d'autres ressources alimentaires que celle représentée par ces campagnols sans que l'on puisse actuellement parler de report de prédation : d'autres micro-mammifères, de la petite faune d'intérêts cynégétique et/ou patrimonial de plaine ou de montagne voir même les espèces de grand gibier (Edwards et al., 2000; Kjellander et Nordström, 2003). Par exemple, Bernard et al. (2010) ont montré que l'effraie des clochers présente un comportement alimentaire opportuniste qui lui permet de consommer des campagnols prairiaux en fonction de leurs densités sur le terrain mais également de se rabattre sur les musaraignes du genre *Sorex* lorsque la ressource en campagnols prairiaux diminue. Dans le cas du lièvre d'Europe, Edwards et al. (2000) indique que la pression de prédation du renard roux sur les levrauts et les individus adultes peut être plus intense lorsque les populations de micro-mammifères sont en phases de basses densités. En république Tchèque, Šálek et al. (2004) ont montré, lors d'une étude sur deux années, qu'après un fort déclin de la communauté de micro-mammifères la prédation sur de faux nids de tétra lyre (*Tetrao tetrix*) a augmenté de 34 à 76%. En Amérique du Nord (Ouest canadien), Brook et al. (2005) ont étudié l'appariement et les couvées du petit fuligule (*Aythya affinis*) et ont ainsi montré qu'il existait une relation statistique entre l'abondance de rongeurs et la productivité du petit fuligule suggérant un report de prédation potentiel sur les couvées. Ces auteurs ont de plus démontré qu'il existait une relation statistique négative entre la productivité du petit fuligule et l'abondance du lièvre d'Amérique (*Lepus americanus*) et posent l'hypothèse d'une pression de prédation partagée entre différentes espèces de proies alternatives en fonction de l'abondance de chacune.

IV - Objectifs de travail

Parmi toutes ces espèces, la petite faune chassable (lièvre d'Europe (*Lepus europaeus*), lièvre variable (*Lepus timidus*), perdrix grise (*Perdix perdix*), caille des blés (*Coturnix coturnix*), tétra lyre (*Tetrao tetrix*)) et patrimoniale (lagopède alpin (*Lagopus muta*), grand tétra (*Tetrao Urogallus*), râle des genêts (*Crex crex*)) représentent à l'heure actuelle des enjeux de gestion et de conservation marqués (Green, 1995; Báldi et Faragó, 2007; Moss et al., 2010; Fernex et al., 2011; Maillard et al., 2012; Cardador et al., 2014; Slamečka et al., 2014; Cardador et al., 2015). En effet, ces espèces, de par les activités anthropiques qui leurs sont associées représentent un enjeu fort pour le développement et l'attrait des territoires ruraux

(activités cynégétiques, tourisme nature). La présence et la gestion raisonnée de ces espèces et des zones de productions herbagères sont génératrices d'emplois directs (Fédérations de chasse, Parcs Naturels Nationaux, Agriculture, industrie laitière) et indirects (13500 salariés dans la production de lait et près de 4000 salariés dans l'industrie laitière en Franche-comté en 2012-2013 (DRAAF, 2014) ainsi que des centaines voir des milliers de salariés non précisément quantifiés dans le tourisme vert ou la protection et l'étude de l'environnement). Le déclin de certaines populations sauvages de ces espèces dans les zones de moyennes montagnes (Edwards et al., 2000; Broyer, 2003; Millot et al., 2012) pose donc un problème environnemental et sociétal fort dans ces territoires ruraux.

Considérant l'exemple du renard roux, il apparaîtrait que les résultats positifs des traitements anti-rabiques en Europe ont entraîné une augmentation des populations de ce prédateur y compris dans les zones de moyenne montagne françaises (Aubert, 1999; Goszczyński et al., 2008; Freuling et al., 2013). L'augmentation de certaines populations de prédateurs généralistes, tel que le renard roux, potentiellement capables d'effectuer un report de prédation sur la petite faune d'intérêts patrimonial et/ou cynégétique pose la question de l'importance des relations proies-prédateurs dans le système « campagnols prairiaux » sur le déclin de certaines espèces telles que le lièvre d'Europe. La présente étude se focalisera sur les campagnols prairiaux, campagnol terrestre (*Arvicola scherman*) et campagnol des champs (*Microtus arvalis*). Les premiers dégâts régionaux de grandes ampleurs liés à des pullulations de ces espèces sont constatés dans le Massif du Jura, comme dans le Massif Central ou la Savoie dès les années 1970 (Airoidi et al., 1989; Airoidi, 1990; Delattre et Giraudoux, 2009; Quéré et Le Louarn, 2011).

Cette thèse a pour but de comparer deux zones géographiques distinctes (vallée alpine de la Haute-Romanche et Massif Jurassien) et présentant un degré a priori différent de connaissances sur les systèmes de pullulations de campagnols prairiaux (vallée alpine de la Haute-Romanche touchée depuis une quinzaine d'années et vierge d'études ciblées comparées au système Jurassien soumis aux pullulations de campagnol prairiaux depuis presque 50 ans et étudié depuis plus de 30 ans). Nous essayerons au travers de ce travail de comparer le phénomène de pullulation observé cette dernière décennie en Haute-Romanche avec les connaissances actuelles et publiées du Massif Jurassien. Nous allons également par l'analyse de données de

monitoring à long terme et la mise en place d'expérimentations de terrain essayer d'apporter des informations quant aux relations entre proies et prédateurs dans un système de pullulation de campagnol prairiaux en milieu tempéré. L'objectif est de tenter une comparaison tant que faire se peut entre les deux zones géographiques pour améliorer la gestion de ces écosystèmes.

Ce travail est organisé autour de chapitres dont chacun vise à répondre aux questions suivantes :

Chapitre 1 :

- Comment a évolué l'occupation du sol en Haute-Romanche entre 1810 et la période actuelle ?
- Quelle était la forme spatio-temporelle de la population de campagnol terrestre en Haute-Romanche entre 1998 et 2010 ?
- Est-ce que la colonisation des parcelles et son intensité étaient liées à l'occupation du sol actuelle ou à son histoire à l'échelle parcellaire ?

Chapitre 2-A :

A l'échelle régionale :

- Est ce que le contexte de pullulation cyclique du campagnol terrestre mène à une plus forte pression de prédation du renard roux sur le lièvre d'Europe ?

Chapitre 2-B :

A l'échelle locale :

- Quelle est l'organisation spatio-temporelle de la population de renard roux de la vallée de la Haute-Romanche ?
- Est-ce que son régime alimentaire est dépendant de la présence de campagnol prairiaux ?
- Est-ce que la distribution spatio-temporelle du régime alimentaire du renard roux est corrélée avec l'organisation spatio-temporelle de la population de campagnols prairiaux ?

Chapitre 3-A :

- Comment les prédateurs réagissent à la présence d'une nouvelle proie alternative dans un système tempéré ?
- Est-ce que cette réponse des prédateurs peut être liée à la variation de l'abondance du campagnol terrestre ou à la structure paysagère ?

Chapitre 3-B :

- Est ce que les résultats obtenus dans le Jura pour le chapitre 3-A sont similaires à ceux obtenus dans la vallée de la Haute-Romanche ?

Chapter I: Historical agricultural changes and the expansion of a montane water vole population in an Alpine valley.

Box 1

Small mammal population outbreaks are one of the consequences of socio-economic and technological changes in agriculture. They can cause important economic damage and generally play a key role in food webs, as a major food resource for predators. The fossorial form of the montane water vole, *Arvicola scherman*, was unknown in the Haute Romanche Valley (French Alps) before 1998. In 1998, the first colony was observed at the top of a valley and population spread was monitored during 12 years, until 2010. Spread occurred as a high population density wave. Based on farming history (1810–2003, 193 years) and spatio-temporal analysis of crop rotations, our study indicates that this montane water vole population outbreak has been promoted by the presence of grassland corridors that increase hayfield connectivity. These corridors appeared as a result of the conversion of cropped fields to hay meadows where montane water vole outbreaks have occurred. Spatial mosaic management for grasslands with decreasing spatial connectedness should be considered to prevent vole outbreak risks and promote biodiversity.

I - Introduction

Agricultural shifts generally correspond with technological and socio-economic changes (Allen, 2000). Mountainous regions are often considered to be favorable to biodiversity and more eco-friendly agricultural practices (Fjeldså et al., 1999). Currently, most areas in Europe have undergone either agricultural abandonment (and subsequent forest recolonization) or specialization (Chemini and Rizzoli, 2003). In developed countries, economic and technological changes in the 1950s led to specialized farming and geographically dissociated animal husbandry from cereal production. Thus, while vegetable and crop productions are now mostly located in the lowlands, farmers in mountainous regions have specialized in growing fodder for animal husbandry and milk production (García-Martínez et al., 2011; Cocca et al., 2012).

Today, in addition to agricultural intensification (increase of productivity in terms of quantity), specialization (production focused only on one or two crop types) is one of the greatest anthropic pressures on biodiversity and ecosystem services (Hole et al., 2005). Thus, while some species that depend on agro-ecosystems are declining (Fuller et al., 2005), others are considered to be pests because of the agricultural losses they cause (Singleton et al., 2010; Koyanagi et al., 2012; Krebs, 2013). The common vole (*Microtus arvalis*) and the montane water vole (*Arvicola scherman*), are widely studied among other species, because both are potential pests to grassland (Krebs 2013).

There are many potential drivers of small mammal population outbreaks, and they are still under debate (Krebs, 2013). Small mammal populations are characterized by high intrinsic growth rates and strong inter-specific competition (Korpimäki et al., 2004). By increasing their food supply, agricultural intensification can promote the growth of small mammal populations (Morilhat et al., 2007). Additionally, agricultural specialization can modify landscape structure and composition, creating physical obstacles to small mammal dispersal or modifying the structure and composition of vole predator guilds (Delattre et al., 1992; Delattre et al., 1996; Giraudoux et al., 1997; Delattre et al., 1999; Duhamel et al., 2000; Morilhat et al., 2008; Falk et al., 2011). Outbreaks may also be driven by weather conditions (White, 2011).

In temperate Europe, early studies on the agricultural damages caused by voles focused on the common vole (*M. arvalis*). Spitz. (1968), for example, reported extremely high damages (87% for Alfalfa and 100% for grass and wheat) in the lowland of Vendée, France after World War II. In mountainous areas, land-use policy led to specialize into grass production and to increase parcel size during the 1960s-1970s (López-i-Gelats et al., 2011). Delattre et al. (1992) reported that multi-annual fluctuations of the common vole increased with the Ratio of Permanent Grassland to Farmland (RPGF). Similarly, in Franche-Comté, France, Giraudoux et al. (1997) found a 5 to 6 year cycle in *A. scherman* population abundance beginning in the early 1970s on regional scale, after the expansion of permanent grassland. For grassland voles, episodic outbreaks become chronic when a scarcity or absence of forest is combined with grassland predominance across the landscape (Delattre et al., 1992) or when the ratio of leguminous plants increases (Spitz, 1972; Delattre et al., 1992). Earlier works have documented that landscape changes may impact the kinetics of rodent populations (Hansson, 1979; Hansson and Henttonen, 1985, Eadie, 1953; Birney et al., 1976). Lidicker (2000) conceptualized these landscape effects with the Ratio of Optimal to Marginal Patch Area (ROMPA) hypothesis. In brief, variation in rodent abundance depends on the prevalence of their optimal habitat within a landscape. In addition, montane water vole outbreaks in Franche-Comté (also in the Massif Central) have been characterized by a spatial spreading over several years (Giraudoux et al., 1997; Berthier et al., 2013) called a traveling wave. Such pattern has also been documented for other species, such as the bank vole (*M. glareolus*) and the field vole (*Microtus agrestis*) in Finland (Hansson and Henttonen, 1985; Ranta and Kaitala, 1997) and the field vole (*M. agrestis*) in Scotland (Lambin et al., 1998; Bierman et al., 2006). However, long-term time-series and large scales data that would permit a detailed study of such processes are rare (Ryszkowski et al., 1971; Ryszkowski, 1982; Erlinge et al., 1982, 1983).

The presence of the montane water vole in the Northern Alps and its sporadic damage to grasslands and orchards are well established (Morel and Meylan, 1970; Meylan et al., 1971; Airoldi, 1976). The geographical complexity of valleys and the high altitude of mountains ranges were previously believed to prevent any large-scale spreading of small mammal outbreaks. The spatio-temporal patterns of montane water vole outbreaks have therefore not yet been documented in this context. In the Haute-

Romanche valley, neither written records (e.g. direct or indirect, from predator diet analysis) nor oral tradition evidenced population outbreaks or even the presence of the montane water vole before 1998, when the first montane water vole outbreak suddenly occurred. Due to its proximity to the Ecrins National Park (*Parc National des Ecrins*, PNE) and the risks of exposing native wildlife to pest chemical control, this outbreak has been carefully monitored and mapped by the PNE staff. A few studies provided very local data describing the presence of the montane water vole in the Northern Alps, but did not mention potential outbreaks in those areas (Morel and Meylan, 1970; Meylan et al., 1971; Airoldi, 1976; Habert, 1988; Lapini and Paolucci, 1992; Saucy, 1994). Thus, the initial colonization of a valley where the species was previously absent has never been studied. The Haute-Romanche valley has undergone major land use changes since the 19th century (Girel et al., 2010; López-i-Gelats et al., 2011). At that time, mixed farming, including cattle husbandry, cereal and potato production was general. The valley began to specialize in animal (cow and sheep) breeding in the 1960s (Girel et al., 2010). In the 19th century, to promote crop production (potatoes, barley, wheat, etc.) and animal husbandry (grazing and mowing) in such challenging conditions, farmers modified the landscape by clearing forests and building field terraces at up to 2000 meters of altitude (Girel et al., 2010). These were abandoned during the 1960s-1970s with subsequent recolonization by grassland.

The aim of this study is to answer the three following questions: How has farmland in the Haute-Romanche valley evolved from 1810 to today? What were the spatio-temporal patterns of the montane water vole population in the Haute-Romanche valley during the 1998-2010 population outbreaks? Was colonization linked to current agricultural practices and/or with individual parcel farming history?

II - Material and methods

II-1 Study site

The study site was in the Haute-Romanche valley (45° 02' 49" N 6° 18' 24" E), located in the sub-alpine and the lower alpine vegetation belts of the Alps (Figure 10). Study site elevation ranged between 1300 meters at the *Fréaux* to 3976 meters at the *Meije* peak. Vegetation is subjected to cold temperatures (mean annual temperature 3.3°C (Bocquet, 2001)), and the growing season is very short (four months) and therefore unfavorable to intensive agriculture. The study area included two municipalities (*Villar*

d'Arène and *La Grave*), which are part of the *Parc Naturel National des Ecrins* (Figure 10). The valley primarily contains pastures (62%), meadows (4%), tillage (< 1%) and larch forest (33%), and there are two main villages and scattered housing (Quétier et al., 2007; Lavorel et al., 2011). Farming mostly consists in breeding *Abondance* cattle for milk production in the neighboring *Savoie* region and breeding sheep for meat production. In summer, high-altitude pastures are grazed by local flocks in addition to a large number of transhumant sheep.

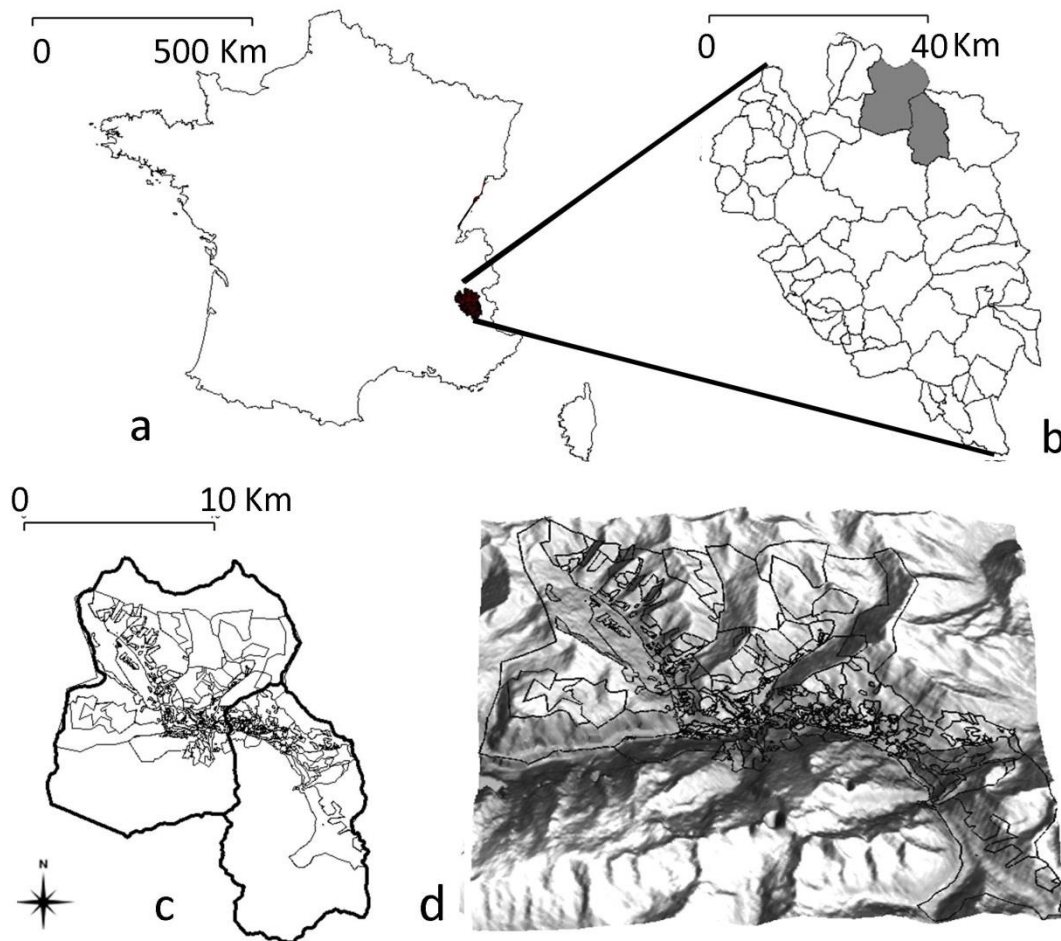


Figure 10 : (a) Parc National des Ecrins (PNE) (in black), (b) La Grave and Villar d'Arène communes (in grey) among the communes of the PNE (c) cadastral parcels in La Grave and Villar d'Arène (d) topography of the area (after Abrams et al., 2010).

II-2 Data collection

II-2-a Simplified Land-use trajectories (SLUT) between 1810 and 2003

Land-use trajectories (LUT) were determined for each individual property (i.e., cadastral parcel) within the *Villar d'Arène* and *La Grave* municipalities. These trajectories were derived from the synthesis of three data sources: interpretation of aerial photographs from 1952, 1960, 1971, 1986, 1994 and 2001, historic data from land-use registers from 1810 and 1970, and recent data from interviews of local farmers in 1996 and 2003 (*Association Foncière Pastorale de Villar d'Arène*, unpublished data) (Quétier et al., 2007; Girel et al., 2010; Lavorel et al., 2011).

Lavorel et al. (2011) combined these data in a Geographic Information System (GIS) and documented past and present land use for the farmed areas within the municipality, using nine LUTs. Based on Lavorel et al. (2011), we simplified the land-use trajectories of the 721 cadastral parcels within the study area into Simplified Land-Use Trajectories (SLUT) (Table 5).

The percentage of each type of land use inside and outside the area where montane water voles were present during the time of the monitoring (1998-2010) was computed in the past and in 2003.

Table 5: Past land-use, land-use in 2003, Land-Use trajectories (LUT) and Simplified Land-Use trajectories (SLUT).

Past Land-Use	Land-use in 2003	LUT	SLUT
Plowed once in the past	Plowed	LUT1	Plowed once in the past and plowed 2003
Plowed once in the past	Mown	LUT2	Plowed once in the past and mown in 2003
Plowed once in the past	Grazed	LUT3	Plowed once in the past and grazed in 2003
Mown once in the past	Mown	LUT4	Mown once in the past and mown in 2003
Mown once in the past	Grazed	LUT5	Mown once in the past and grazed in 2003
Mown once in the past	Unexploited	LUT6	Mown once in the past and unexploited in 2003
Grazed once in the past	Grazed	LUT7	Grazed once in the past and grazed in 2003
Unexploited	Unexploited	LUT8	Unexploited in the past and unexploited in 2003
Grazed once in the past	Grazed	LUT9	Grazed once in the past and grazed in 2003

II-2-b Montane water vole monitoring

The staff of the *Parc Naturel National des Ecrins* monitored and mapped the abundance of montane water voles in the Haute-Romanche Valley each year from 1998 to 2010 after the melting of the snow. The entire region was traveled to determine the spatial distribution and relative abundance of surface indices (earth tumuli, runways, etc.) via direct observation. Indices were scored using the following scale, adapted from Giraudoux et al. (1995):

- 0 : No activity on the surface
- 1 : Isolated indices
- 2 : < 50% of the area colonized
- 3 : > 50% of the area colonized

The method used did not mean to represent the true abundance, but the activity of the montane water vole population. Giraudoux et al. (1995) have shown that this kind of index can be used as a proxy of relative abundance. Continuous areas with the same score were mapped as a polygon and stored in GIS as ESRI shapefiles. Polygons were then rasterized at a 5 m resolution for map algebra.

II-3 Temporal dynamics of the abundance of montane water voles at the cadastral-parcel scale

We computed the mean abundance score of each cadastral parcel in each year. For each cadastral parcel, we determined the first year with a mean abundance score above 0, which was considered to be the last year before the vole population outbreak. Montane water vole abundance dynamics from the first date of colonization of a parcel could thus be represented by this categorization, regardless of the geographical position of the parcel. Moreover, on the cadastral parcel scale, we studied the relationships between the intensity of the outbreak, the current land use (i.e., in 2003) and the SLUT.

II-4 Spatial spread of montane water vole population

We calculated the yearly speed of the population spread by measuring the minimal Euclidian distance between the most geographically advanced frontline at year “n” and the most advanced frontline at year “n + 1”.

II-5 Statistical analysis

We studied the annual variation of montane water vole abundance since parcel colonization, with abundance index as the response variable and year as an independent variable. We took possible non-linearities into account using a General Additive Mixed-effect Model (GAMM) (Wood, 2006). Using GAMM allowed us to break the total variation into (i) the variation due to the fixed effect (here, the relationship between the response variable and the independent variable, $f_i(x_i)$) (ii) variation due to a random effect (here, the repetition of montane water vole abundance estimates on the parcel over time, $Z_i b_i$) and (iii) the residual variation of the model, Δ_i . Overall, the model relies on a link function, g (here, Gaussian), linking the response variable to the independent variable by the relationship:

$$g(E(Y)) = X_i \theta + f_1(x_1) + f_2(x_2) + \dots + f_m(x_m) + Z_i b_i + \Delta_i$$

$X_i \theta$ is a row of the model matrix for any strictly parametric model component (Wood, 2006), and $f_i(x_i)$ is a nonparametric smoothing function (e.g., the sum of continuous sections of cubic polynomial splines calculated so that they are joined at points called nodes or knots) or a parametric function (without smoothing).

(2) The effects of current land use and SLUT were examined using a linear mixed model with the abundance index of montane water voles as the response variable, the current land use and SLUT categories as fixed effects, and parcel as a random effect to account for repeated measurements of each parcel. The relationship was the following:

$$y_i = X_i \beta + Z_i b_i + \Delta_i$$

For statistical inferences, we used a permutation test ($n=1000$) to avoid overestimating the degrees of freedom if spatial auto-correlation was present.

(3) The relationship of the minimal distance covered by montane water voles (y_i) and year (x_i) was calculated using a simple linear model.

We checked the validity of our model by comparing its AIC scores with that of a null model (Burnham and Anderson, 2002). To compare the values obtained for each category within our independent variables, we compared the AIC scores that we obtained to the null model.

II-6 Computing environment

Spatial analysis and GIS data management were conducted in Quantum GIS 1.8.0-Lisboa (Quantum Gis, 2013), GRASS GIS 6.4.2 (Grass Development Team, 2012) and R 2.15.1 (R-Core Team, 2012b) using the packages car (Fow and Weisburg, 2011), foreign (R-Core Team, 2012a), maptools (Lewin-Koh et al., 2012), mgcv (Wood, 2011), pgirmess (Giraudoux, 2012), raster (Hijmans and Van Etten, 2012), rgdal (Keitt et al., 2012), rgeos (Bivand and Rundel, 2012), Rlab (Boos and Nychka, 2012), and sp (Bivand et al., 2008).

III - Results

III-1 Past and present land use

In the past, grazed parcels were located at the highest altitudes, while mown and/or plowed parcels were located at the lowest altitudes within the Haute-Romanche Valley. Plowed parcels were generally in close proximity to settlements. By 2003, grazed areas had extended toward the valley bottom and settlements. Plowed areas had virtually disappeared, and mown areas decreased considerably.

Within the range of the montane water vole (from 1998 to 2010), the amount of mown area did not dramatically change (34.4% of the farmland area in the past compared with 34.6% in 2003, Figure 11). However, outside of the montane water vole's range, the amount of mown area decreased from 8.8% in the past to 0.9% in 2003. Plowed areas declined both inside and outside the montane water vole's range, from 40.5% to 0.5% and 1.7% to 0.02%, respectively. Conversely, grazed areas increased both inside and outside the montane water vole's range, from 18.4% to 58.2% and from 53.4% to 63%, respectively.

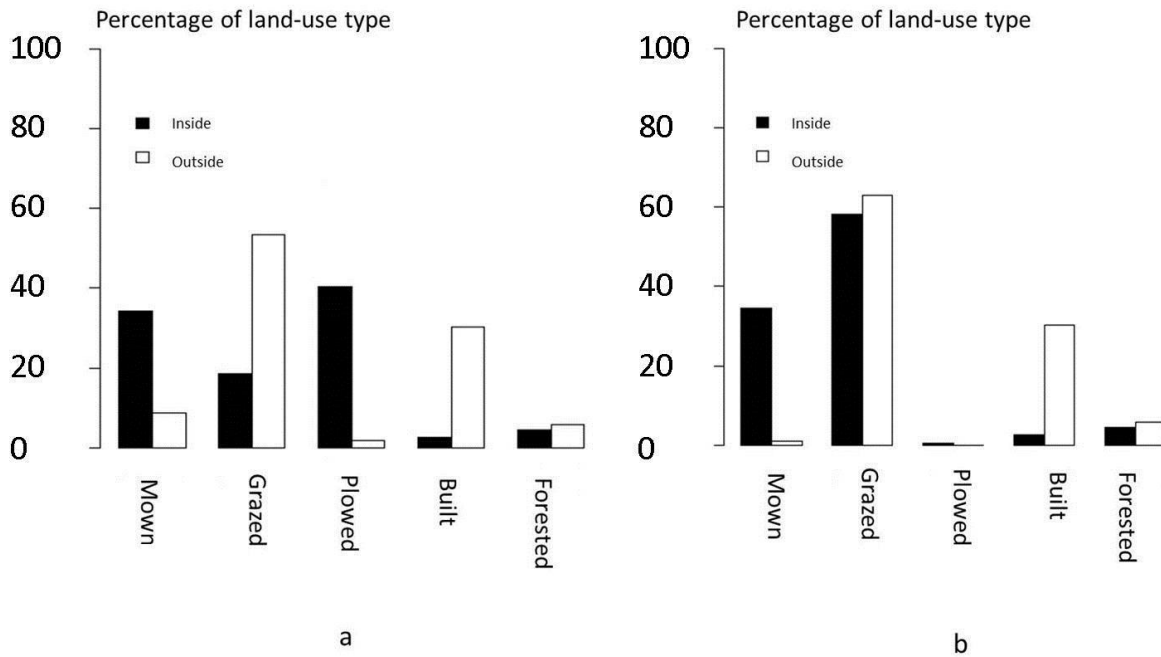


Figure 11 : Percentage of each type of land-use inside (black) and outside (white) of the area of presence of the montane water vole (1998-2010) in the past (a) and in 2003 (b).

III-2 Temporal dynamics of montane water vole abundance

Figure 12 displays the inter-annual variations of *A. scherman* abundance, according to the 2003 land-use categories. There was generally a dramatic increase in abundance during the year of colonization, peaking that year or the following, and then a slow decrease to low densities over the following 5 years (P -value < 0.0001).

The average abundance of *A. scherman* significantly differed among the 2003 land-use categories ($R^2 = 0.02$; $\Delta AIC = 33$, PermTest P -value < 0.0001) and was significantly lower in grazed than in mown parcels ($\Delta AIC = 27$, Coef = - 0.03).

The abundance of montane water voles also differed among SLUT categories ($R^2 = 0.03$; $\Delta AIC = 49$). Parcels grazed in the past and continuing to be grazed in 2003 had a significantly lower abundance of montane water voles than the other parcels ($\Delta AIC = 45$, Coef = - 0.38).

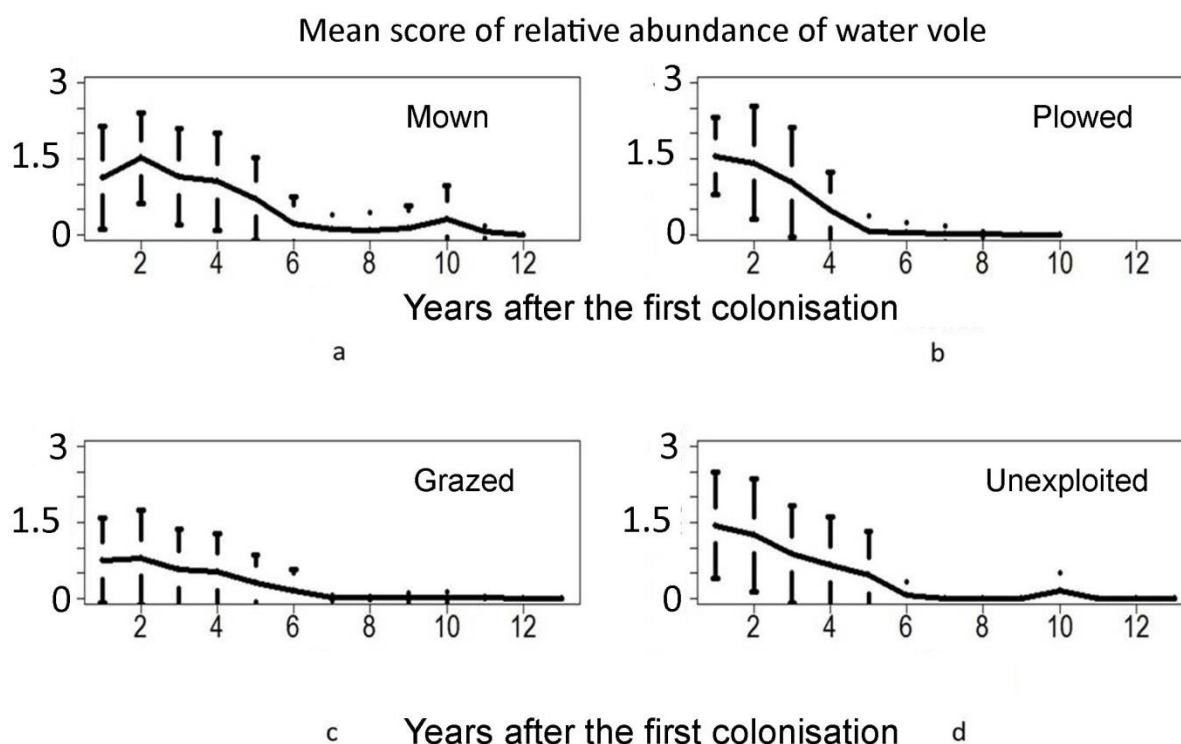


Figure 12 : Time variation of the mean score of montane water vole abundance for each parcel, from first colonization, according to land-use in 2003 (a: Mown, b: Plowed, c: Grazed, d: Unexploited).

III-3 Spatial spread of the montane water vole population

The first vole colonies were observed in 1998, near the *Chalet de la Buffe*. Other colonies were detected three years later, near the *Hameau de Valfroide*. The vole colonization front moved from these two epicenters toward *La Grave* village within 5 years. The bottom of the Haute-Romanche Valley was reached in 2003, and the colonization front moved toward the *Col du Lautaret* through the *Villar d'Arène* village (Figure 13). The general direction of colonization was northwest to southeast, following the Haute Romanche Valley. However, the direction of spreading changed three times: southeast to northwest between 1998 and 1999, southeast to northwest between 2003 and 2004 and southeast to northwest between 2005 and 2006.

The distance covered each year by the montane water vole population significantly differed between years ($\Delta AIC = 197$; $R^2 = 0.22$) (minimum = 500 meters per year, median = 1500 meters per year, maximum = 3700 meters per year).

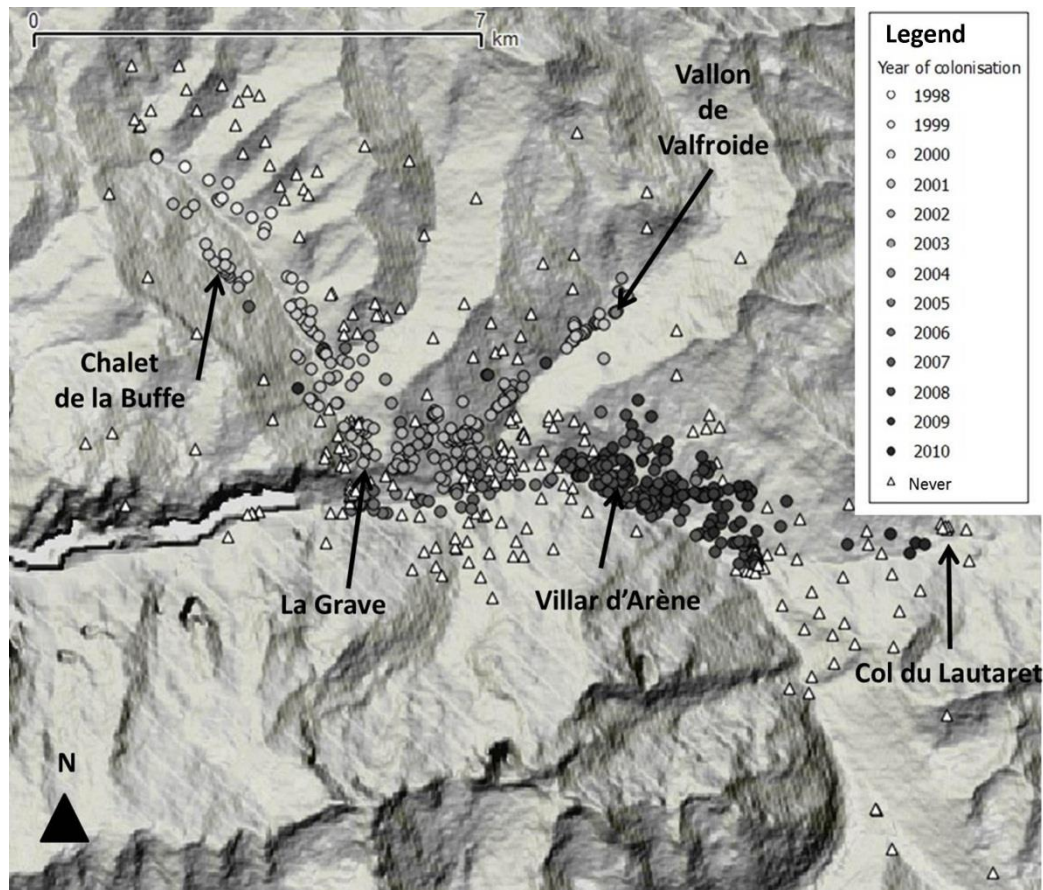


Figure 13 : Colonization by the montane water vole between 1998 and 2010.

IV - Discussion

IV-1 Past and present land use

In the past, areas that were distant from villages and farms were generally inaccessible to livestock, due to elevation and slope. Therefore, temporary settlements were established in summer pastures, and cattle and sheep were relocated to the valley during the winter months. Areas that were mown or plowed were close to farms in the valley bottom. The spatial organization of the Haute-Romanche valley reflects traditional land use patterns in mountainous regions worldwide (Nyssen et al., 2009; Girel et al., 2010; Pôças et al., 2011; Negi et al., 2012). Between 1810 and 2003, the landscape of the Haute-Romanche valley changed, following patterns consistent with most other Alpine valleys. Farming specialization in livestock breeding extended former grazing areas and led to a large decrease in mown areas for technical and economic reasons (subsidies sometimes made it more viable to purchase hay for cattle feed than to produce it locally on steep slopes) (Leynaud and Georges, 1965; Girel et

al., 2010). An increase in farmer incomes during the second half of the 20th century and the concomitant expansion of the market to supra-regional scales led to the abandonment of subsistence and cash crop farming, thus leading to a dramatic decrease in plowed areas (Girel et al., 2010). Agricultural specialization is common in most mountainous regions worldwide to varying degrees (Huijun et al., 2002; Chemini and Rizzoli, 2003; García-Martínez et al., 2011). For example, in the Jura Mountains, grassland surface area represented approximately 40% of the total farmland in 1956 but approximately 100% in 1988 (Giraudoux et al., 1997). Similarly, Tasser et al. (2009) report that until the 1960s, the montane belt in South Tyrol (Italy) was composed of a mosaic of arable fields and grasslands, and shifted to 100% grasslands in the subsequent years. In Switzerland, over the same period, Maurer et al. (2006) showed that low-intensity grasslands farther from settlements were abandoned, whereas easily accessible grasslands were used more intensively (Kahmen et al., 2002) and were mown and fertilized more frequently (Bätzing, 2003).

In the Haute-Romanche valley, the amount of mown area within the montane water vole range did not change between 1810 and 2003. This finding may be important because high grass in mown areas for several months prior cutting is more favorable to the montane water vole than low grass of pastures and plowed fields (Morilhat et al., 2007).

IV-2 Temporal dynamics of montane water vole abundance at the cadastral-parcel scale

The montane water vole population outbreak from 1998 to 2010 in the Haute-Romanche valley is similar in terms of temporal patterns to other areas where cyclic outbreaks occur (e.g., the Jura and the Massif Central Mountains). Considering the temporal aspect of the outbreak locally, we demonstrated a quick population increase (one year) in abundance followed by a non-linear slow decrease over the subsequent years. In western Europe, montane water vole populations are usually cyclic, with a period of 5 to 7 years (Saucy, 1994; Giraudoux et al., 1997; Berthier et al., 2013). Here, we monitored the montane water vole population of the Haute-Romanche valley over thirteen years. At the parcel scale, we recorded only one outbreak during the first six years of observation. Moreover, we observed peak abundance during the very first year of colonization. One possible hypothesis is that the method we used (i.e., scoring

very large areas with the minimal possible effort) may have led us to miss the earliest stage of colonization at the parcel scale. Alternatively, colonization of new parcels may have led to an explosive increase in the local population.

IV-3 Spatial spread of montane water voles during parcel colonization

Parcel colonization spread in a northwest to southeast direction in a traveling wave, from *La Buffe* (a valley bottom more or less locked by the higher altitude areas of the *plateau d'Emparis* and the *Pic du Mas de la Grave* range) to the village of *La Grave*, then to the village of *Villar d'Arène*, and finally dying off at the *Col du Lautaret*. However, this spreading receded three times. The first time (from 1998 to 1999), it encountered the slopes of the *Mas de la Grave* range, which peaks at 3000 meters. The second time, receding took place between two villages (from 2003 to 2004) and the third time in an area with deep gullies (from 2005 to 2006). Here, the inhabited areas and gullies appeared to be obstacles to the montane water vole spread, corroborating the findings of Berthier et al. (2013) in the Jura Mountains.

Traveling waves of montane water vole populations have also been studied in the Jura Mountains (Giraudoux et al., 1997; Berthier et al., 2013). Berthier et al. (2013) observed a spreading speed of 7.4 km per year in a northwest to southeast direction, radiating away from a major landscape discontinuity. In our study, the maximum annual distance covered was less than 4 km. Models indicate that landscape heterogeneities are instrumental in generating traveling waves because landscape heterogeneities impact vole dispersal (Sherratt et al., 2003; Johnson et al., 2004). When modeling large-scale landscape features, including absorbing boundaries (in which individuals who encounter obstacles perish), these models tend to show that the spatio-temporal dynamics of a colonization include perpendicular movement away from obstacles (Sherratt et al., 2003). This assumption is supported by our observation that montane water vole spreading in the Haute-Romanche valley receded three times after encountering obstacles, such as inhabited areas, gullies or steep slopes. In the Jura range, changes in montane water vole population abundance were monitored over 16 years (from 1989 to 2004) over a large area ($> 2500 \text{ km}^2$). Using graphical analyses and abundance data from an entire demographic cycle (from 1989 to 1994), Giraudoux et al. (1997) suggested that outbreaks emerge from epicenters located in a southwestern to northeastern strip of land and then spread as a traveling wave from the

northwest to southeast over more than 2500 km² at a speed exceeding 10 km per year. In our study, we observed a similar process, in which colonization began very locally (i.e., the bottom of the *vallée de la Buffe*) and spread (but at a lower speed than that in the Jura Mountains). Berthier et al. (2013) demonstrated that this direction of the wave's movement (northwest to southeast) supports the idea that landscape obstacles generate a process similar to traveling waves. Similarly, the colonization of the Haute-Romanche valley occurred in a northwest to southeast direction, which was orthogonal to the potential obstacles surrounding the valley (i.e., peaks, forest, and gullies). Indeed, in the Jura Mountains, the montane water vole traveling wave also moved orthogonally to large-scale obstacles in the southeast and northwest; the waves' longitudinal axis was perpendicular to the direction of the waves (80° to 90°). In the Jura Mountain study, landscape discontinuities (e.g., subalpine mountain range, large forests, rugged terrain, lakes, and plowed land (Morilhat et al., 2007, 2008)) were unsuitable for montane water vole populations. Similarly to Giraudoux et al. (1997) and Berthier et al. (2013), we found that even on a comparatively small scale (10 km² against 2500 km²), the traveling waves of montane water vole colonization were strongly shaped by natural (gullies, stiff slopes) and human (settlements) obstacles.

IV-4 Impact of current land use and SLUT on montane water vole abundance during parcel colonization

Here, we show that the area of plowed fields, a habitat unfavorable to montane water voles (Morilhat et al., 2007), dramatically decreased in the Haute-Romanche between 1810 and 2003. This trend may explain the unimpeded spread of the montane water vole population along the valley, across the *La Grave* and *Villar d'Arène* villages. During this period, the amount of mown areas remained unchanged where the montane water vole colonization occurred. Mown areas are known to be more favorable to montane water vole populations (Morilhat et al., 2007). Furthermore, grazed parcels had lower montane water vole abundance during our study, which is consistent with previous findings reported by others (Morilhat et al., 2007). For instance, Morilhat et al. (2007) found that tramping by cattle and low grass height were highly unfavorable to montane water vole populations.

In our study, grazed parcels had lower montane water vole abundance than other parcels with any other land-use history. This finding indicates that land-use trajectories

have no measurable effect on the montane water vole outbreak or colonization; instead, current land use appears to be the key-factor (e.g., the disappearance of plowed areas and the stability of mown areas where montane water vole outbreak occurred). The relationship between land use and topography may also drive montane water vole population spread. Valley bottoms, where the mown area remained stable and plowed in the past, have gentle slopes and relatively deeper soil, which is more favorable to montane water voles (Airoldi, 1976; Morilhat et al., 2007). In the Haute Romanche valley, topography and current land use can be assumed to be the main drivers of colonization, similar to patterns observed in the Jura Mountains (Berthier et al., 2013). By providing ample resources and shelter and by channeling vole dispersal, mown areas increase optimal habitat connectivity.

IV-5 Origin of montane water voles

Girel et al. (2010) demonstrated that the landscape of the Haute-Romanche valley was already dominated by grassland in 1960. However no montane water vole outbreak was reported until 1998. Actually, this outbreak coincides with the first record of the species in the valley. This finding is crucial because other areas in France where montane water vole outbreaks occur are also areas where montane water voles have been present for a long time (Butet and Spitz, 2001). This raises the question of where the first montane water vole colonizers came from. The species was known to be present in neighbouring valleys further north in Savoie. The genetic characterisation of populations and a phylogeographic approach (Taberlet et al., 1998) would be essential to track the way the species may have colonized the Haute Romanche valley.

V - Conclusion

Recent land use changes in the Haute Romanche valley are characterized by the abandonment of plowing, the stabilization of mown areas at the valley bottom and the increase of grazed areas. Here, we describe the first colonization of a valley complex that was likely free of *A. scherman* before 1998. This colonization shows similarities with the cyclic population variations reported in the Jura and the Massif Central Mountains, corroborating the idea that montane water vole colonization and outbreaks follow the same general pattern across regions. Our results corroborate earlier findings (Delattre et al., 1992, Giraudoux et al., 1997; Luque-Larena et al., 2013; Jareño et al., 2015) stressing about the role of historical changes of practice and landscape in

triggering grassland small mammal outbreaks. This strengthens the notion that landscape management can be a way to regulate grassland small mammal populations. Parcel colonization followed a northwest to southeast gradient, and followed a pattern similar to that of traveling waves. We provide evidence that the spread receded three times, most likely due to the landscape structure. This finding illustrates the role of physical obstacles at the landscape scale. Finally, we showed that the driver of outbreak development is most likely to be current than historical land use. It appears that grazing limits the intensity of the outbreak and that, conversely, mown areas could be favorable to the montane water vole population, as they are in the Jura Mountains. Considering that mown areas are now being promoted by National and European Agri-Environmental Schemes to increase biodiversity, it may be important to promote spatial mosaic management for grasslands (e.g., a heterogeneous mosaic of mown, grazed and plowed areas, decreasing spatial connectedness) to take into account vole outbreak risks and biodiversity issues. However, such a management strategy may be difficult to organize, especially considering mowing in space and time, livestock grazing, etc. To develop a management scheme that takes these constraints into account will be a challenge for researchers, conservationists and farmers.

Chapter II: Montane water vole outbreak consequences on generalist predator demography, diet and alternative food resources.

Box 2

The main objective of this work was to study the impact of grassland vole outbreaking population on predators and their alternate food resources. In this second chapter we aimed at answering the followings:

- Can a cyclic montane water vole population outbreak context lead to a more intense predation pressure of the red fox on the brown hare?
- Is there a seasonal dependence in spatial red fox faeces deposition pattern in Haute-Romanche valley?
- Is the red fox diet similar in Haute-Romanche and the Jura Mountains, to areas where *A. scherman* population outbreaks occur?

To that aim, we worked both in the Alpine valley and in the Jura Mountains with two different approaches (i) long-term monitoring of vole/fox/hare populations, respectively (ii) red fox dietary analysis and) In the Jura Mountains we looked for correlations between the relative abundance of three species (e.g. red fox, brown hare and montane water vole) at regional scale. After detrending the red fox and the water vole time series for long term variations and controlling for the effect of rodenticide treatments on red fox abundance, we observed (i) statistically significant negative correlations on one hand between red fox and brown hare relative abundance, and on the other hand between montane water vole and red fox relative abundance and (ii) positive correlation between montane water vole and brown hare relative abundance. However, between 1% and 3% of the total variations were explained by those statistical relationships, indicated that if a diet switching from red fox to brown hare cannot be excluded, it would explain a nominal part of the variation of brown hare abundance on this scale. Furthermore, no red fox dietary analysis was carried out to know whether the red fox as the key predator concerned. In the Alpine valley context, we collected red fox faeces to study red fox dietary composition. With the same sampling pressure, we collected 4 to 5 times more faeces in October than in July with a lower distance between faeces and villages in October than in July. Our results are congruent with earlier authors who showed that red fox diet composition variation was seasonal. We also showed the importance of insects in the diet of foxes in this area, compared to the Jura mountains where fox diet is much less diversified.

A - Introduction

In chapter I, we showed that montane water vole outbreaks are strongly land-use dependent in the Alps similarly as in the Jura and the Massif Central mountains. We showed that the intensity of montane water vole outbreaks was higher in mown grassland areas. One potential consequence of montane water vole outbreaks could be a diet switching of generalist predators during decline phase and potential predation pressure increase on alternative food resources as the brown hare.

Here, we had the opportunity to study the long term trend of fox and brown hare populations in the Doubs department where outbreaks of *Arvicola scherman* populations and subsequent control based on rodenticide treatment occur. We want to know if a cyclic montane water vole population outbreak context can lead to a more intense predation pressure of the red fox on the brown hare. In such a context, the hypothesis is that a negative correlation should be found between the abundances of the brown hare and the red fox, taking into account the relative abundance of the montane water vole (the main prey) and taking into account the continental trends of the two populations. Indeed, red fox and brown hare population dynamics are strongly continental with long term trends perceived at this scale characterised by a general increase for red fox and decrease for brown hare (Edwards et al., 2000; Schweiger et al., 2007). The abundance of the mountain water vole and the possible effects of secondary poisoning of foxes due to bromadiolone treatment against voles (Jacquot et al., 2013).

Furthermore, in the Haute-Romanche valley, we had the opportunity to collect fox faeces during a low density phase of *Arvicola scherman* populations. The aim of this study is to answer the two following questions: Is there a seasonal dependence in spatial red fox faeces deposition pattern in Haute-Romanche valley? Is the red fox diet similar in Haute-Romanche and the Jura Mountains, to areas where *A. scherman* population outbreaks occur?

Chapter II (A): Montane water vole (*Arvicola scherman*) outbreaks and variation of abundance of brown hare (*Lepus europaeus*) and red fox (*Vulpes vulpes*) in Jura Mountains.

I - Introduction

Cynomys spp., Ochotonidae (Delibes-Mateos et al., 2011) and vole populations can provide a very important biomass in some ecosystems. This biomass may represent a food resource for their predators, including endangered and hence protected species (Löfgren et al., 1986; Korpimäki, 1989; Amar et al., 2003; Hörnfeldt, 2004; Lanszki and Heltai, 2011; Coeurdassier et al., 2012). Thus, understanding the role of those preys in food webs has become central in the assessment of natural or anthropic effects in the ecosystems where small mammal population outbreak occurs (Gilg et al., 2003; Ekerholm et al., 2004). Some predators like the red fox (*Vulpes vulpes*) are considered as generalist predators because they switch their diet according to food availability (Padial et al., 2002; Russell and Storch, 2004; Dell'Arte et al., 2007; Sidorovich et al., 2009). Generalist predator functional response in a grassland vole outbreak context might lead to a diet switching to an alternate prey in decline period. In some pest species dynamic driven systems, the generalist predator diet switching to alternate preys allows the sustainability of the predator population density (Holt, 1977; Hardwood and Obrycki, 2005; Koss and Snyder, 2005). In Europe, the red fox is known to switch its predation effort on alternate preys (Marchesi et al., 1989). Dealing with the brown hare (*Lepus europaeus*), Edwards et al. (2000) indicate that the red fox predatory pressure on leverets and adults could be more intense during small mammal low density periods.

In temperate systems like in the Jura Mountains, among several factors, red fox demography could have been driven by anthropic actions such as secondary poisoning or large scale rabies treatment. Jacquot et al. (2013) showed correlative evidence that rodenticide field treatment has reduced the red fox population densities in the Doubs Department. These authors showed, at regional scale, that red fox abundance variation was linked with rodenticide treatment intensity. Jacquot et al. (2013) hypothesized that, after intensive rodenticide treatments, red fox populations could

recover because of higher recruitment rates into impacted populations due to decreased intraspecific competition (Heydon and Reynolds, 2000) or by recolonization of red foxes in the impacted area from neighbouring areas less intensively treated. In Europe, successive rabies control campaigns have led to rabies incidence reduction (more than 90% reduction in detected cases at European scale and 100% in the case of France) within 10 years (Freuling et al., 2013). Aubert (1999), Goszczyński et al. (2008) and Freuling et al. (2013) showed that considerable red fox population increase was linked to rabies control.

Already reported as an important hunted species by Gérard (1871), the brown hare has strongly declined in Europe since 1960 because of agriculture changes, diseases and hunting (Frölich et al., 2003; Santilli and Galardi, 2006; Pépin and Angibault, 2007; Cardarelli et al., 2010; Runge et al., 2011). Prey-predator relationships are also often mentioned as one additional cause (Rizzotto and Focardi, 1997; Reynolds and Tapper, 1995; Reynolds et al., 2010). Agricultural low-productive area abandonment concomitant to intensification, homogenization and mechanization of high productivity areas are among the most often cited causes of the brown hare decline (Péroux, 1995; Santilli and Galardi, 2006; Cardarelli et al., 2010). Zoonosis (Edwards et al., 2000; Frölich et al., 2003; Santilli and Galardi, 2006) could lead to lethal or sub-lethal effect on the brown hare. Relationship between the brown hare and the red fox has been already studied (Reynolds and Tapper, 1995; Rizzotto and Focardi, 1997). In Denmark, Schmidt et al. (2004) showed that the brown hare long-term decline could be explained by the red fox population increase. Reynolds et al. (2010), after a predator's guild control (*Vulpes vulpes*, *Mustela erminea*, *Mustela nivalis*, *Rattus norvegicus*, *Corvus corone corone*, *Pica pica*, *Corvus frugilegus* and *Corvus monedula*) observed an increase in the brown hare population density. Moreover, Edwards et al. (2000) indicated that predation pressure on the brown hare could be regulated by the small mammal abundance variation. Hunting effect on brown hare populations seem contrasted in the literature according to various authors. Indeed, in Santilli and Galardi (2006), populations are shown to be hunting pressure resilient and the effect of hunting is low. Conversely, modelling indicates that hunting pressure can be the most important factor in some declining brown hare populations (Péroux et al., 2005).

The aim of this study was to answer the following questions: Can a cyclic montane water vole population outbreak context lead to a more intense predation pressure of the red fox on the brown hare? In such a context, the hypothesis is that a negative correlation should be found between the abundances of the brown hare and the red fox, controlling for other ecological factors. To answer this question, we researched for correlations between the brown hare (the alternate prey) and the red fox (the predator) taking into account continental population trends of both brown hare and red fox population, the relative abundance of the montane water vole (the main prey), and potential red fox secondary poisoning by bromadiolone treatments.

II - Material and Methods

II-1 Study area

The study was set in the Doubs department (47°10'N, 06°25'E), 5 234 km² in north-eastern France. The altitude ranges from about 200 to 1463 meters. The climate is continental in lowland and mountainous in altitude. Agriculture is characterized by mixed farms in lowland and meadows in altitude. Forests are deciduous in lowland and coniferous in mountains (Badré and Demolis 1997; Corvol, 2002). The study area presents four geomorphological features: (1) a plain at 200-400 m altitude with the Doubs river valley lower part; (2) a first plateau at 400-700 m; (3) a second plateau at 700-900 m altitude; (4) a mid-altitude mountainous area between 900 and 1463 m altitude (Giraudoux et al., 1997).

II-2 Data collection

II-2-a Monitoring of brown hare and red fox

Counting of red fox and brown hare was performed by the volunteers of the *Fédération Départementale des Chasseurs du Doubs* on a protocol designed with the support of the University of Bourgogne-Franche-Comté (P. Giraudoux). Countings were carried out for three successive nights in each early spring between 2004 and 2011 before vegetation growth to ensure maximum visibility. The number of transects (Figure 14) were 470 (2009), 471 (2008), 472 (2007), 475 (2004, 2005, 2006, 2010, 2011) and transect length ranged from 609 to 3891 meters (mean = 1340 ± 406 meters). These methods were already used by earlier authors such as Reynolds and Tapper (1995);

Raoul et al. (2003); Ruelle et al. (2003). Road transects were traversed by car at a maximum speed of 20 km per hour. Both sides of the car were lightened with a 100-watt spot. The relative abundance is the KAI (Kilometric Abundance Index) which is the maximum number of animals observed per kilometre during the three nights.

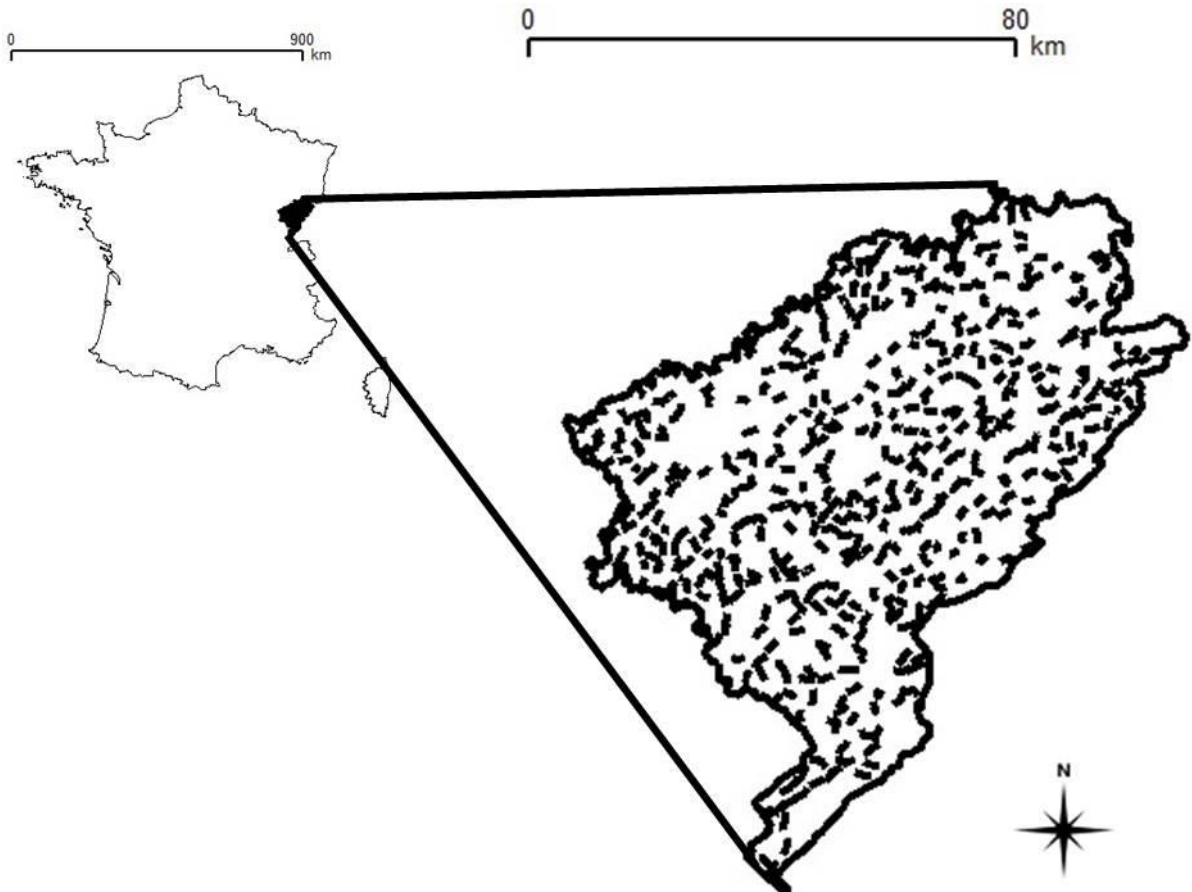


Figure 14 : Study area and night transects for the monitoring of brown hare and red fox in the Doubs department.

II-2-b Monitoring of montane water vole

Each commune of the department, each year in the autumn was scored by professional observers of the *Fédération régionale de défense contre les organismes nuisibles* (FREDON). The method developed to assess vole abundance was based on the scoring of earth mounds tumuli density that reflects vole activity (“colony” locations) and is roughly proportional to montane water vole abundance (Giraudoux et al., 1995, 1997). Vole abundance was recorded on the commune scale based on the following categories: 0 = no colony, 1 = some isolated colonies, 2 = colonies present in many

grasslands, 3 = very numerous colonies and serious damages to grassland. This index method provides reliable information to describe qualitatively, or semi-quantitatively, the spatiotemporal variation in vole abundance (Berthier et al., 2013). We used the data collected between 2002 and 2009. We assumed that the montane water vole abundance variation indirectly impacts the brown hare abundance and, if any, would be better measured with a two-year time lag. For example, with a montane water vole outbreak during the autumn of the year **n-2**, the predation pressure variation on leverets would occur during the spring of the year **n-1**, and the leveret survival measurable during the monitoring at the end of the winter or the early spring of the year **n**.

II-2-c Spatial interpolation of KAI at commune scale

Montane water vole estimates and night road side counts were not carried out on the same sampling units (respectively communes, and road transects). Therefore, we interpolated KAI values for each commune based on transects.

Ordinary kriging was used to assign KAI values per commune each year from 2004 to 2011 (regular trend surface from 2006 to 2011 data): KAI values from transects were interpolated on the centroids of communes. Ordinary kriging uses variogram models of spatial autocorrelation to provide spatially weighted estimators (Bivand et al., 2008). Omnidirectional empirical variograms were computed each year. Variographic envelopes, which test for potential absence of spatial autocorrelation, were computed by permuting geographical coordinates among KAI records ($n = 99$ simulations), recalculating the empirical variogram for each simulation and plotting the maximum and minimum semivariance obtained at each lag. Empirical variograms were fitted, using weighted least squares (Cressie 1985), with one correlation function (exponential). Kriged interpolations were additionally mapped on a regular grid (2-km mesh).

After checking the absence of spatial autocorrelation by using variogram representation of our geographical data of brown hare and red fox KAI values, we computed trend surface map for each year and for each species on the Doubs department scale. The aim was to interpolate the KAI value of transects on the centroids of each commune based on a 2-kilometre grid which is the most representative distance between two transects and the centroids of communes. We

chose to use a General Additive Model (GAM) to predict the value because of a great flexibility to adapt to the possible non-linearity of the data (Wood, 2006). Overall, the model relies on a link function g (normal, Poisson, binomial, etc.). Linking the response variable to the independent variables by the relation:

$$g(E(Y)) = X\beta + f_1(x_1) + f_2(x_2) + \dots + f_m(x_m)$$

$f_i(x_i)$ is a nonparametric smoothing function (eg sum of continuous sections of cubic polynomial splines calculated so that they are joined at points called nodes - knots -) or parametric (without smoothing). The validity of the trend surface thus obtained is determined by comparing the score GCV (Generalized Cross Validation) (Wood, 2006) between GAM model below:

$$\text{gam}(z \sim s(x, y, k = n)) \text{ and null model : } \text{gam}(z \sim 1)$$

where z is the transect's KAI, x the transect's longitude, y the transect's latitude and k the numbers of knots choose to optimized our model.

II-3 Statistical analysis

We used a General Additive Mixed Effect model to assess the effect of several independent variables (commune, time, rodenticide treatments, montane water vole relative abundance) pulled or considered independently on red fox and brown hare relative abundance variation and the correlation between red fox and brown hare relative abundance. Red fox and brown hare population dynamics are strongly continental with long term trends perceived on this scale (general increase for red fox, decrease for brown hare) (Edwards et al., 2000; Schweiger et al., 2007). To keep it in, the analysis might provide a confusing factor for a regional-scale analysis. We analysed KAI temporal variation in order to detrend the respective KAI and remove the KAI variation on commune scale in our model, the computation of the brown hare and the red fox KAI represents a spatio-temporal repetition of the monitoring at the commune scale. Thus, the variable « commune » was introduced in the model as a random variable. Using a General Additive Mixed Effect model allows us to consider singly the part of the variation of the fixed effect – here the relation between our

response variable and our previously cited independent variables –, the part of the variation of the random effect – here the own variation of the repetition of the monitoring of the brown hare and the red fox at the commune scale – and the residual part of the model. In our study area, the red fox population dynamic is strongly rodenticide dependent. In 2003 rodenticide treatments caused firstly a decline in red fox abundance (Jacquot et al., 2013). Then, with the decrease in treatment intensity, Jacquot et al. (2013) observed a red fox population recovery. We noticed the effect of the treatment during the autumn of the year **n-1**.

The null hypothesis is that there is no correlation between red fox and brown hare relative abundance controlling for other independent variables. We checked the validity of our models by comparing its AIC score with the one of a null model (Burnham and Anderson, 2002). We only considered the communes which were monitored, at least once, both for water vole abundance and the rodenticide. This represent 394 communes (Figure 15).

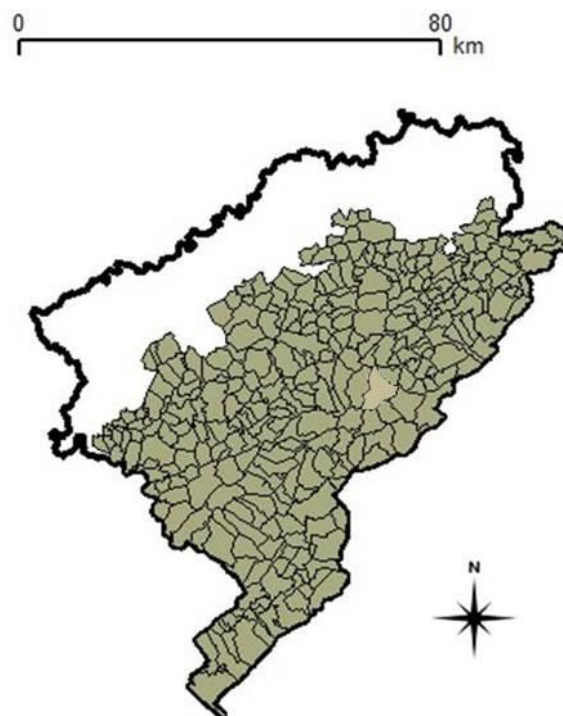


Figure 15 : Studied communes monitored, at least once, both for water vole abundance and the rodenticide.

II-4 Computing environment

Analysis was done using R 2.12.0 (R-Core Team, 2012b) with the following packages: ade4 (Dray et al., 2007), chron (James and Hornik, 2011), date (Therneau et al., 2011), doBy (Højsgaard et al., 2012), foreign (R-core, 2011), geoR (Ribeiro and Diggle, 2001), gplots (Warnes et al., 2011), maptools (Lewin-Koh et al., 2010), mgcv (Wood, 2011), nlme (Pinheiro et al., 2010), pgirmess (Giraudoux, 2012), rgdal (Keitt et al., 2010), rgeos (Bivand and Rundel, 2012), sp (Bivand et al., 2008).

III - Results

III-1 Brown hare and red fox detrending

Figures 16a and 16b show a temporal trend both in the brown hare and red fox KAI and of the red fox KAI variation ($p\text{-value} < 0.01$; $0.14 < R^2 < 0.20$). It appears that kriged values of brown hare have declined and that the red fox one has increased.

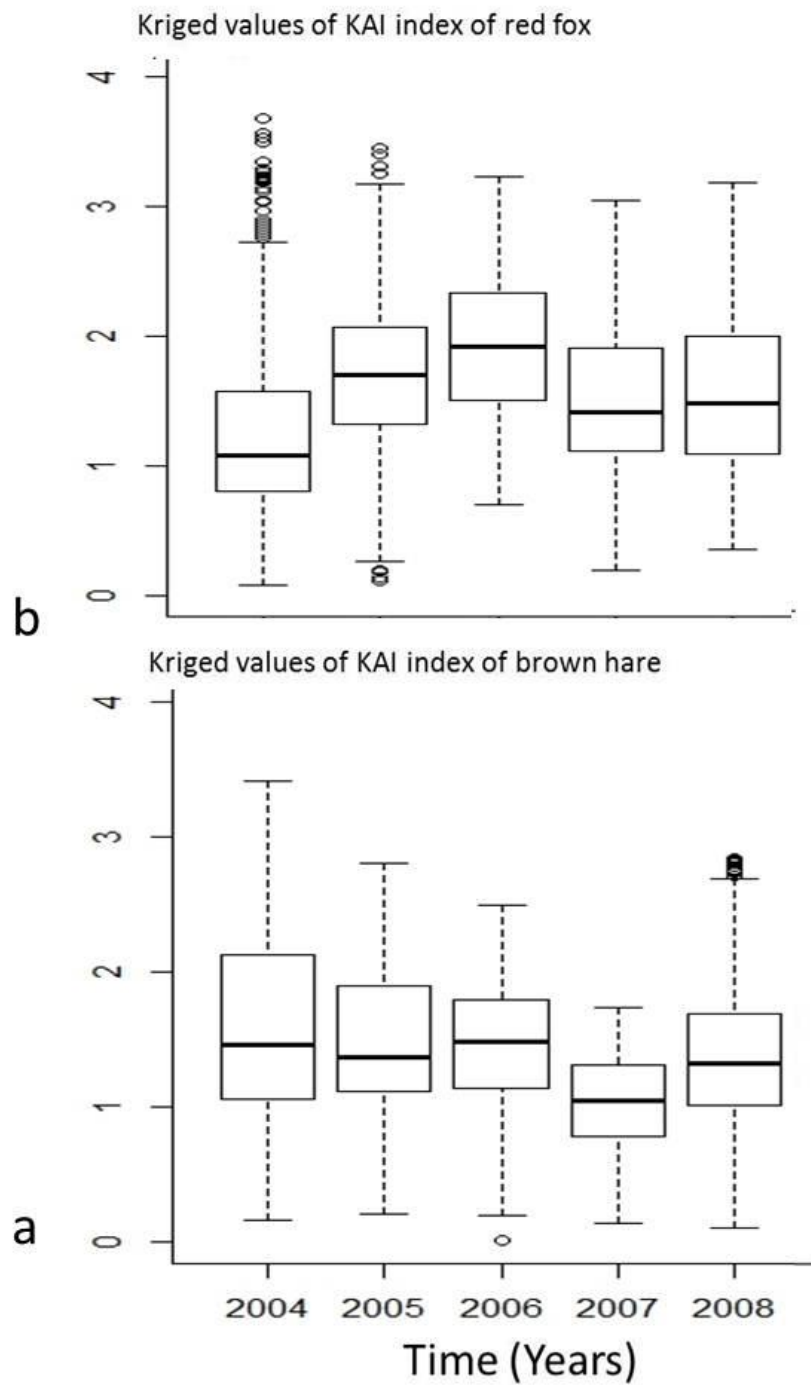


Figure 16 : Red fox (b) and brown hare (a) KAI variation over time.

Moreover, figures 17b and 17c show red fox and brown hare KAI are spatially structured.

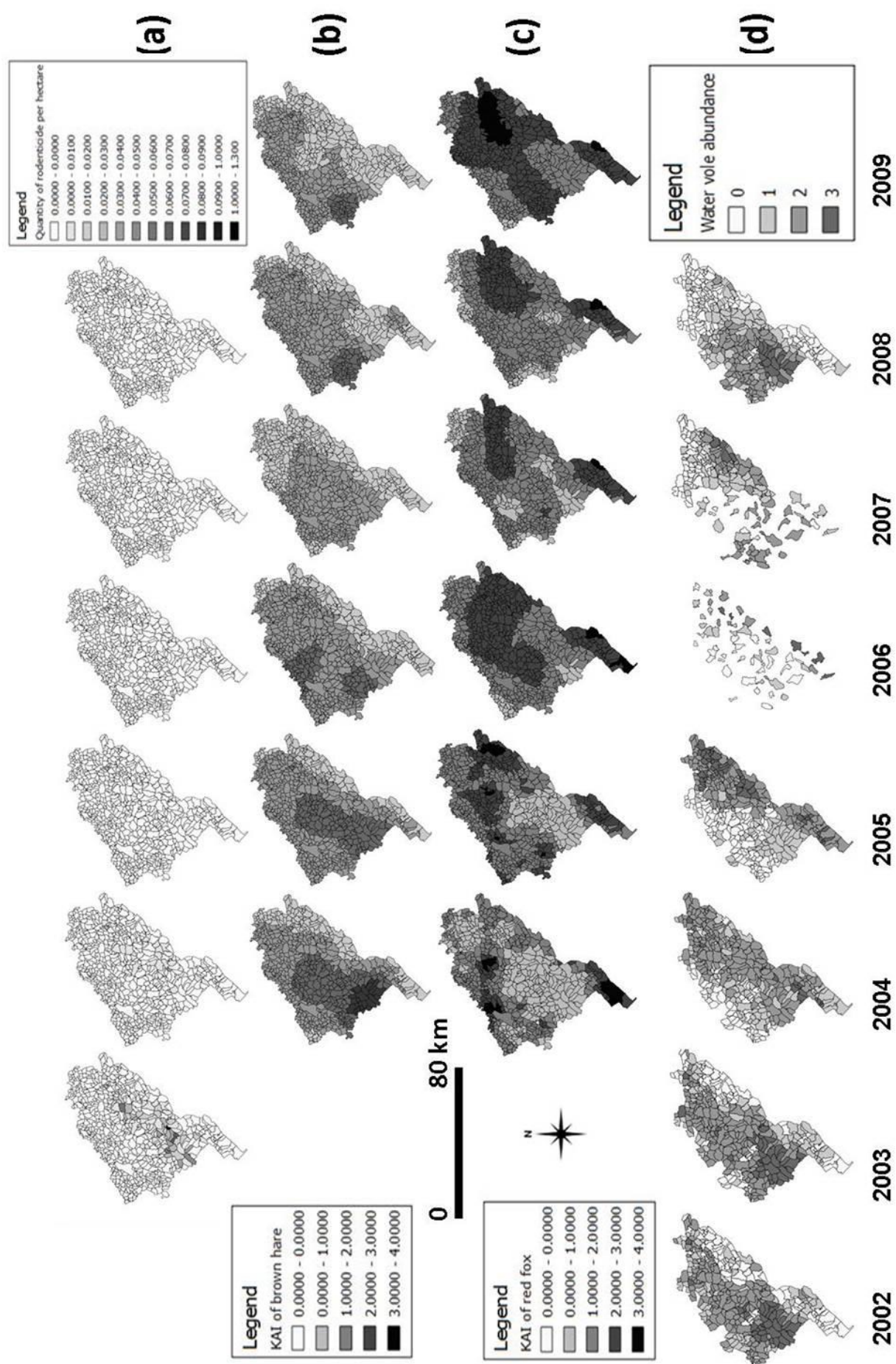


Figure 17 : Rodenticides quantity used (a), KAI of brown hare (b), red fox (c), montane water vole (d) variation between 2002 and 2009.

III-2 Rodenticide induced red fox KAI variation

Our results show an impact of the rodenticide treatments on the detrended red fox KAI variation ($p\text{-value} < 0.01$; $R^2 = 0.02$) (Figure 18). The correlation between detrended red fox KAI and rodenticide treatments is parabolic with a detrended red fox KAI increasing from a very low level one year after the first high rodenticide treatment in 2003 and declining after the second-high rodenticide treatment in 2006.

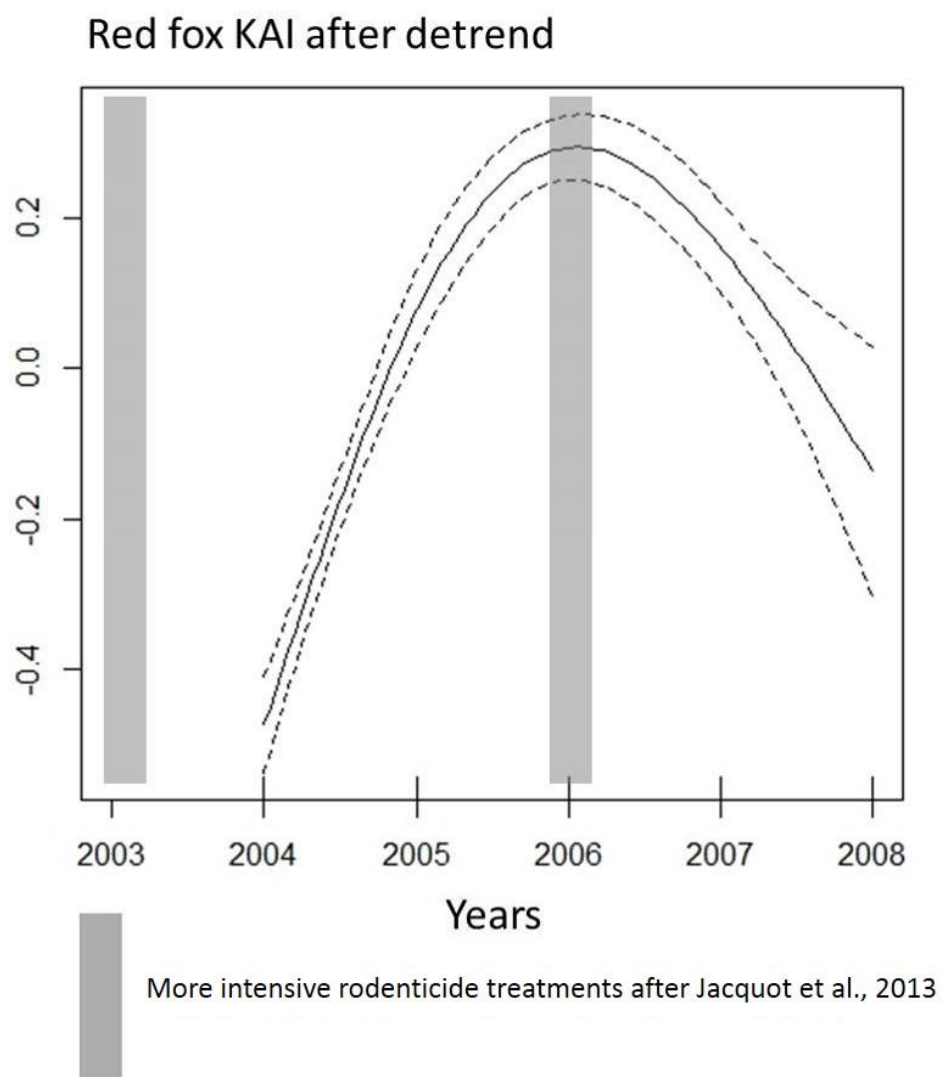


Figure 18 : Relationship between detrended red fox KAI and rodenticide treatments.

III-3 Brown hare and red fox relationship

Our results show a negative non-linear correlation between detrended brown hare KAI and detrended red fox KAI controlling for the effect of rodenticide treatments (Figure 19) (p -value < 0.01 ; $R^2 = 0.03$). More the red fox KAI increase more the brown hare KAI decrease.

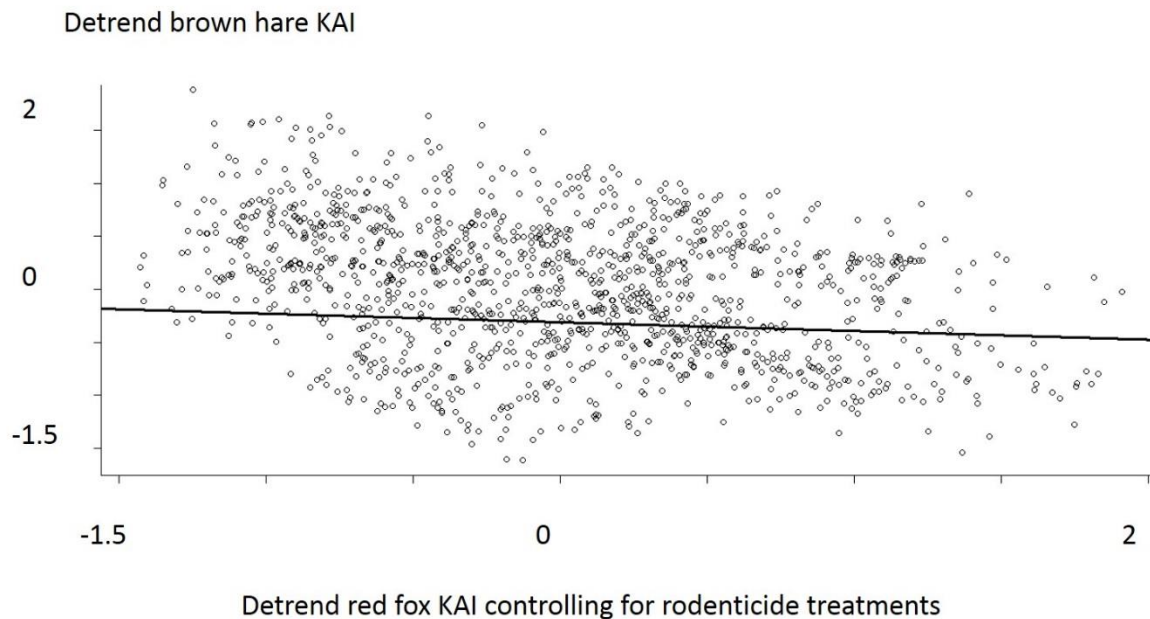


Figure 19 : Relationship between detrend brown hare KAI and detrend red fox KAI controlling for rodenticide treatments.

III-4 Brown hare and red fox KAI and montane water vole abundance

The Figure 20 shows that there is a positive relationship between the water vole relative abundance and the detrend brown hare KAI (p -value < 0.01 ; $R^2 = 0.01$). The higher the montane water vole abundance the higher the brown hare KAI. Our results also show a statistical correlation between the water vole relative abundance on the detrend red fox KAI controlling for the effect of rodenticide treatments (p -value < 0.01 ; $R^2 = 0.01$).

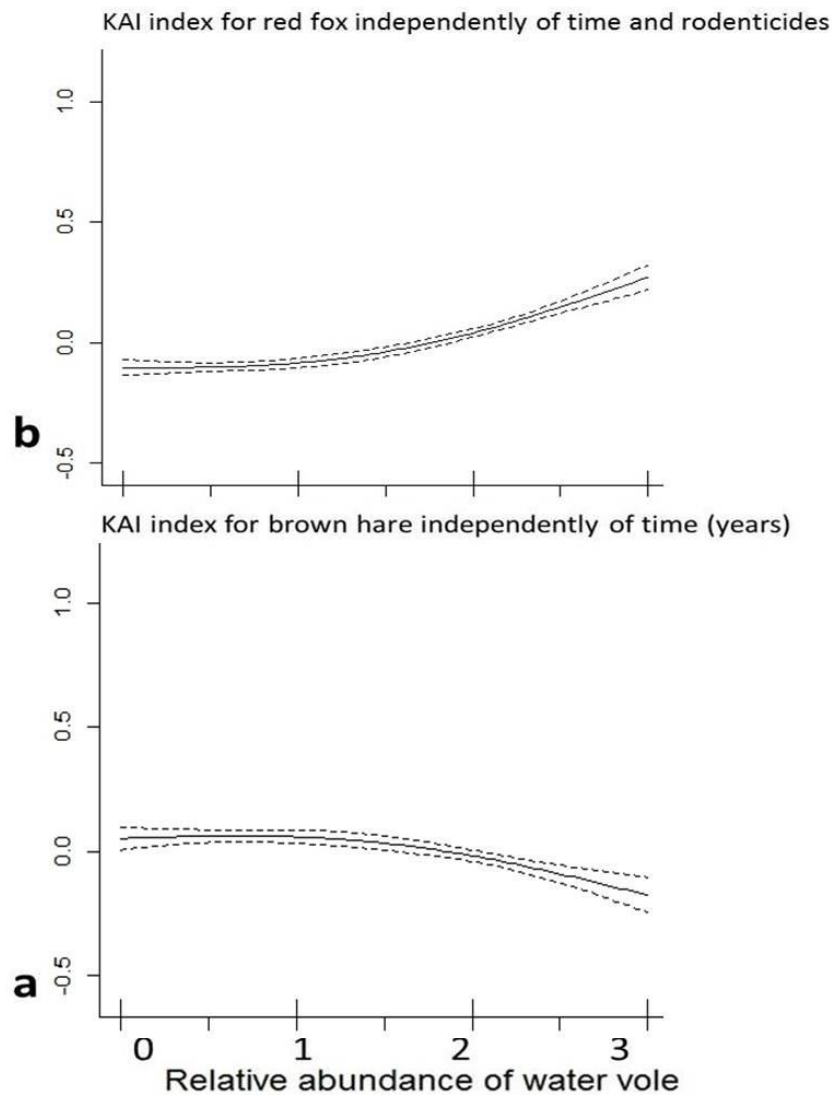


Figure 20 : Variation of detrended brown hare KAI (a) and detrended red fox (b) KAI without effect of rodenticide treatments linked to the montane water vole relative abundance.

IV - Discussion

IV-1 Brown hare and red fox detrending and rodenticide induced red fox KAI variation

Considering kriged values of red fox and brown hare KAI, our results confirm the assumption that these abundances present significant and opposite long term temporal trends in the study area. Aubert (1999) claimed that in Europe, and more particularly in the Jura Mountains, the success of rabies control in red fox populations led to an increase of this population. As a matter of fact, we observed that red fox KAI on the regional scale (the Doubs department) is increasing.

We also observed a parabolic relationship between detrended red fox KAI and rodenticide treatments with a red fox KAI increasing one year after the first intensive rodenticide treatment in 2003 and declining right after the second less intensive rodenticide treatment in 2006 (Jacquot et al., 2013). This observation could be a consequence of the potential recovery of regional red fox population depressed by secondary poisoning observed in 2003 and 2006 as showed by Jacquot et al. (2013). Therefore, the existence of secondary poisoning because of rodenticide treatments is known in several species of montane water vole predators (Berny et al., 1997, 2005; Berny and Gaillet, 2008; Guitart et al., 2010; Tosh et al., (2011, 2012); Christensen et al., 2012; Rattner et al., 2012).

Considering our results, two hypotheses (continental trend and red fox population recovery) seem to be plausible because of the existence of relationships between red fox KAI variation and time or rodenticide treatments.

IV-2 Brown hare and red fox relationship

At the regional scale, our results show a statistically significant and negative relationship between detrended brown hare KAI and detrended red fox KAI controlling for rodenticide treatments.

In fact, the red fox KAI variation explains 3% of the brown hare KAI variation in a context of montane water vole cyclic outbreaks. This variation is less important than those reported by Wincentz (2009) who showed on the Danemark scale that brown hare and red fox bags are negatively linked. The author indicates that red fox bag variation explains 14% of the brown hare bag variation and suggest that other factors such as habitat quality or climate must have driven brown hare population dynamic. Indeed, Wincentz (2009) explained that when the leveret production rate is high, the losses due to predation could be balanced by the brown hare population reproduction.

IV-3 Brown hare or red fox KAI and montane water vole abundance

Our results show a significant and positive statistical link between a high montane water vole relative abundance and a high brown hare KAI. In several studies on the effect of generalist predators on *tetraonidae* in a context of small mammal cyclic outbreaks, an indication of potential diet switching is the existence of a positive relation

between the abundance of the small mammal and either the production of fledglings for the Capercaillie (Leclercq et al., 1997). Even if, in this study, we observed both positive correlation between the montane water vole and the brown hare abundance and a negative one between the brown hare and the red fox abundance, we lack evidence of the red fox dietary data during this period to fully conclude to a diet switching.

In terms of dietary analysis, within 3 years of diet analysis on red fox faeces, Giraudoux et al. (2002) showed that the brown hare remains represent 3% of the diet without being able to find a statistically significant difference before and after a common vole (*Microtus arvalis*) population decline. In Poland, Panek (2009) studied the diet composition in red fox den during reproduction. He confirms a positive effect of the high brown hare abundance on the adult hare remain proportion in a den. He also found a statistically significant and negative impact of vole abundance on adult hare remain proportion in a den for a 9-year survey and analysis. This last study confirms similar results obtain by Goszczyński and Wasilewski (1992).

Here, we can conclude that (i) on a regional scale, controlling for continental trends and other confusing factors, the higher the red fox KAI, the lower the brown hare KAI and that (ii) there is an indication of potential diet switching from montane water vole to brown hare without being able to determine which predator(s) is(are) concerned. However, this significant correlation explains a very little fraction of the variations of abundance of the brown hare.

V - Conclusion

In this study, we showed the brown hare and the red fox abundances present opposite temporal trends in the study area. Considering the trend of the red fox, we were able to find a parabolic relationship between red fox KAI and rodenticide treatments with a red fox KAI increasing after the intense high rodenticide treatment in 2003 and declining after the second less intense rodenticide treatment in 2006. Two hypothesis of a positive continental trend led by rabies control and red fox population recovery after rodenticide treatments seem to be plausible. Considering these first results in the brown hare and the red fox population dynamics, we observed at the regional scale a negative correlation between detrended brown hare KAI and red fox KAI. Considering

the very low part of explained variance of this correlation and the literature, this result confirms that other factors driving brown hare population dynamics should exist. We also observed a positive relationship between a high montane water vole relative abundance and a high brown hare KAI indicating a potential diet switching from montane water vole to brown hare. However, because of the absence of red fox diet data during the study, we were not able to have direct evidence of a diet switching.

Chapter II (B): Seasonal variation of the red fox (*Vulpes vulpes*) diet in the low density phase of *A. scherman*.

I - Introduction

The red fox is generally described as a generalist and opportunistic predator. Its diet has already been described in numerous different systems such as farmland (Dell'Arte et al., 2007), Mediterranean mountain (Padial et al., 2002), continental high mountain (Cagnacci et al., 2003), middle mountain (Raoul et al., 2010), woodland (Sidorovich et al., 2006), semi-arid environment (Dell'Arte and Leonardi, 2005), urban area (Contesse et al., 2004). Considering the Jura Mountains, the red fox diet is well described by numerous studies (e.g. Giraudoux, 1991; Weber and Aubry, 1993; Ferrari and Weber, 1995; Weber, 1996; Raoul et al., 2010; Jacquot, 2013) with the descriptions of the correlations between diet composition and grassland vole abundance (for some examples see: Giraudoux, 1991; Weber and Aubry, 1993; Ferrari and Weber, 1995; Raoul et al., 2010; Jacquot, 2013).

The study of red fox ethology and ecology depends on animal density estimation and/or animal activity pattern. Both direct and indirect methods have been used to study the red fox population and/or activity (Cavallaini, 1994; Webbon et al., 2004). Due to legal and technical difficulties to mark animals, counts of marked individuals are generally not suitable for large-scale surveys. The alternative methods such as spotlight counts or culling have been used to monitor red fox populations (Jacquot et al., 2013). However, these methods pose several limits (biased density estimation, culling effort dependent). Because of their cost-efficiency, indirect methods are potentially more convenient for large-scale surveys. Some studies (Cavallaini, 1994; G  thlin et al., 2012) present faeces counting as a reliable method for computing relative index of density of red fox. However, faeces counts may be confused the persistence times due to weather conditions, diet-related differences in the red fox defecation, seasonal or habitat differences in deposition patterns (Beltr  n et al., 1991; Cavallaini, 1994).

Alpine studies on red fox diet showed that the red fox diet was concentrated over ungulates, small rodents, fruits and insects. Ungulates (mostly carrions) were consumed during the cold season as a key-food resource (Cagnacci et al., 2003).

During the warm season, small mammals replaced ungulates according to their seasonal availability (e.g. Delattre et al., 1986). In the study of Lucherini and Crema (1994), the red fox fed on garbage and earthworms during the cold season because of ungulate scarcity while in the warm season it fed on insects and fruits as alternative food resources. This pattern explains the great seasonal overlap of trophic niches in the red fox. However, the use of these different food resources fluctuates depending on studies: invertebrates, e.g. insects and earthworms were a rich seasonal food item in Lucherini and Crema (1994) while in Cagnacci et al. (2003), insects were a seasonally important category but earthworms were never detected in scats. Leinati et al. (1960) did not report the presence of invertebrates in the fox diet. However, the red fox diet information in the Alpine mountains concerns very local studies and has never been linked with a field measure of grassland vole abundance (Leinati et al., 1960; Cavallini and Lovari, 1991; Lovari et al., 1994; Lucherini and Crema, 1994; Cagnacci et al., 2003). However, those studies concern Italian Alps and we did not find information on red fox diet in French Alps

The aim of this study is to answer the following questions: Is there a seasonal dependence in spatial red fox faeces deposition pattern in Haute-Romanche valley linked with the potential seasonality in food resources? Is the red fox diet similar in Haute-Romanche and the Jura Mountains to areas where *A. scherman* population outbreaks occur?

II - Material and methods

II-1 Study site

The study area is the Haute-Romanche valley as presented in Chapter 1.

II-2 Red fox-like faeces sampling

Red fox-like faeces were collected for dietary analyses in summer (from July 22th to 27th) and autumn (from October 7th to 10th) 2013 and in summer (from July 7^h to 10th) and autumn (from October 6th to 10th) 2014 mainly in open landscapes along road verges and paths. Approximately 80 kilometres of road verges/paths were sampled in each session (Figure 21a). Each transect was searched for faeces only once. Red fox – like faeces were identified on the basis of diameter, shape and odour (Bang and

Dahlstrom, 1974). Each faeces was geo-referenced using Global Positioning System (GPS)).

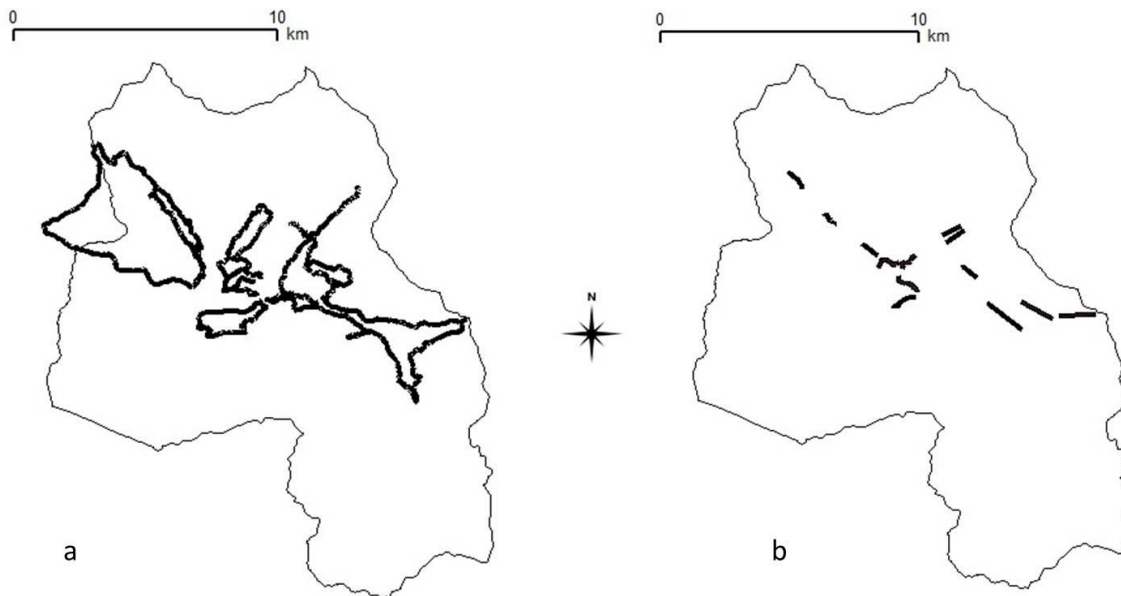


Figure 21 : Transect of red fox-like faeces sampling (a), small mammal transects (b).

II-4 Host faecal test

Visual identification to species was verified using PCR methods. The methodology was developed by Dinkel et al. (2011). First, DNA was extracted from faecal samples (500 mg), then we performed a Quantitative Polymerase Chain Reaction (qPCR) with specific primers respectively from the red fox, the domestic cat (*Felis catus*) and the dog (*Canis familiaris*).

II-5 Macro-remains analysis

Each faeces were processed for dietary analysis. Faeces were first decontaminated by autoclaving in a wet atmosphere at 180°C for 30 minutes and then left overnight in a pot containing water. After homogenisation, an aliquot of 5 mL of water was taken to investigate the presence of earthworms' chaetae using a stereomicroscope (X36 magnification). Faeces were then washed with water above a sieve (500 μ mesh size) to isolate the macroscopic undigested remains. Identification of small mammal remains was carried out by examining teeth (Le Louarn and Quéré, 2003). Voles of the genus *Microtus* (i.e. *Microtus arvalis*, *Microtus agrestis*, *Microtus nivalis*, *Microtus multiplex* and *Microtus subterraneus*) could not be separated because of the low quality of the bone and teeth remains. They were identified as *Microtus* spp., *M. arvalis*, a grassland

species, that is more likely to be predated than the other species with much lower population density. Therefore, the following categories were used in our study: undetermined voles, *Microtus* spp., *A. scherman*, undetermined small mammals, undetermined meso- or macro-mammals, undetermined mammals, bird, undetermined arthropod, orthoptera, coleoptera, fruit/cereal, earthworm and others (for example, plastic). The categories were recorded for each faeces on a presence/absence basis and the results expressed as the frequency of occurrence (percentage of the total number of faeces with the presence of the item in each site) as recommended by Zabala and Zuberogitia (2003).

II-7 Statistical analysis

We used a simple linear model to compare Euclidean distance between the red fox-like faeces and the villages between the four periods of faeces sampling.

II-8 Computing environment

Spatial analysis GIS data managing have been done with Quantum GIS 1.8.0-Lisboa software (Quantum Gis, 2013); GRASS GIS 6.4.2 (Grass Development Team, 2012) et R 2.15.1 (R-Core Team, 2012b).

Others data management were performed with R 2.12.0. software: used package: car (Fow and Weisburg, 2011), foreign (R-Core Team, 2012a), maptools (Lewin-Koh et al., 2012), mgcv (Wood, 2011), pgirmess (Giraudoux, 2012), raster (Hijmans and Van Etten, 2012), rgdal (Keitt et al., 2012), rgeos (Bivand and Rundel, 2012), Rlab (Boos and Nychka, 2012), sp (Bivand et al., 2008).

III – Results

III-1 Host faecal test

We tested 88 faeces and we found that 98% were from red fox origin. The 2% remaining correspond to other animal such as cat or dog.

III-2 Number and distribution of red fox-like faeces

We collected 23 red fox-like faeces in July 2013 (Figure 22a), 109 in October 2013 (Figure 22b), 18 in July 2014 (Figure 22c) and 100 in October 2014 (Figure 22d) for a total of 250.

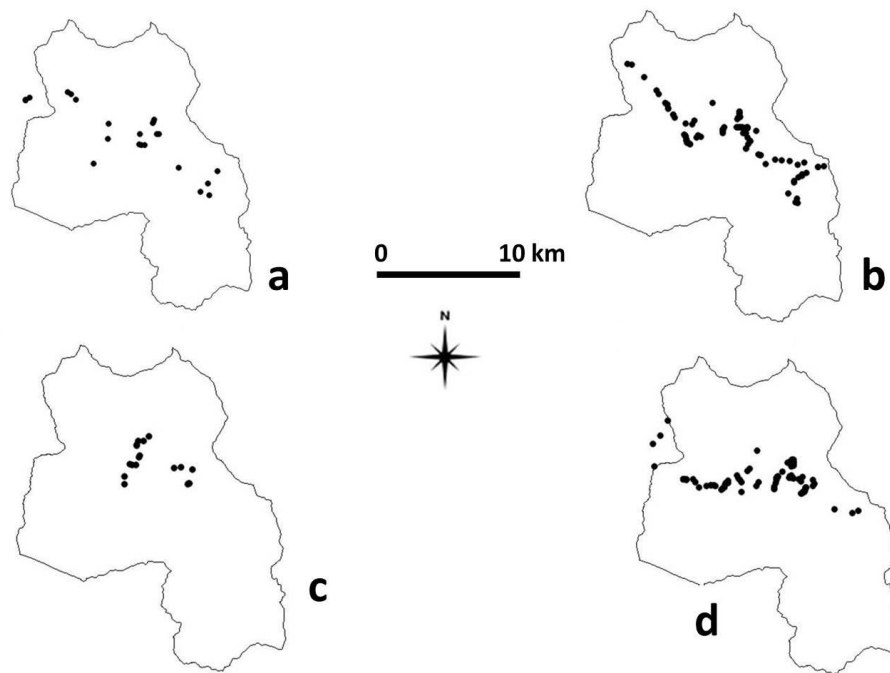


Figure 22 : Spatial distribution of the red fox-like faeces in July 2013 (a), October 2013 (b), July 2014 (c) and October 2014 (d).

Statistically significant differences were observed between the average distance of red fox faeces and villages: 1382m (+/- 884) in July 2013 against 798m (+/- 617) in October 2013 and 1035m (+/- 538) in July 2014 against 978m (+/- 797) in October 2014 ($0.0003 < p\text{-value} < 0.01$) (Figure 23).

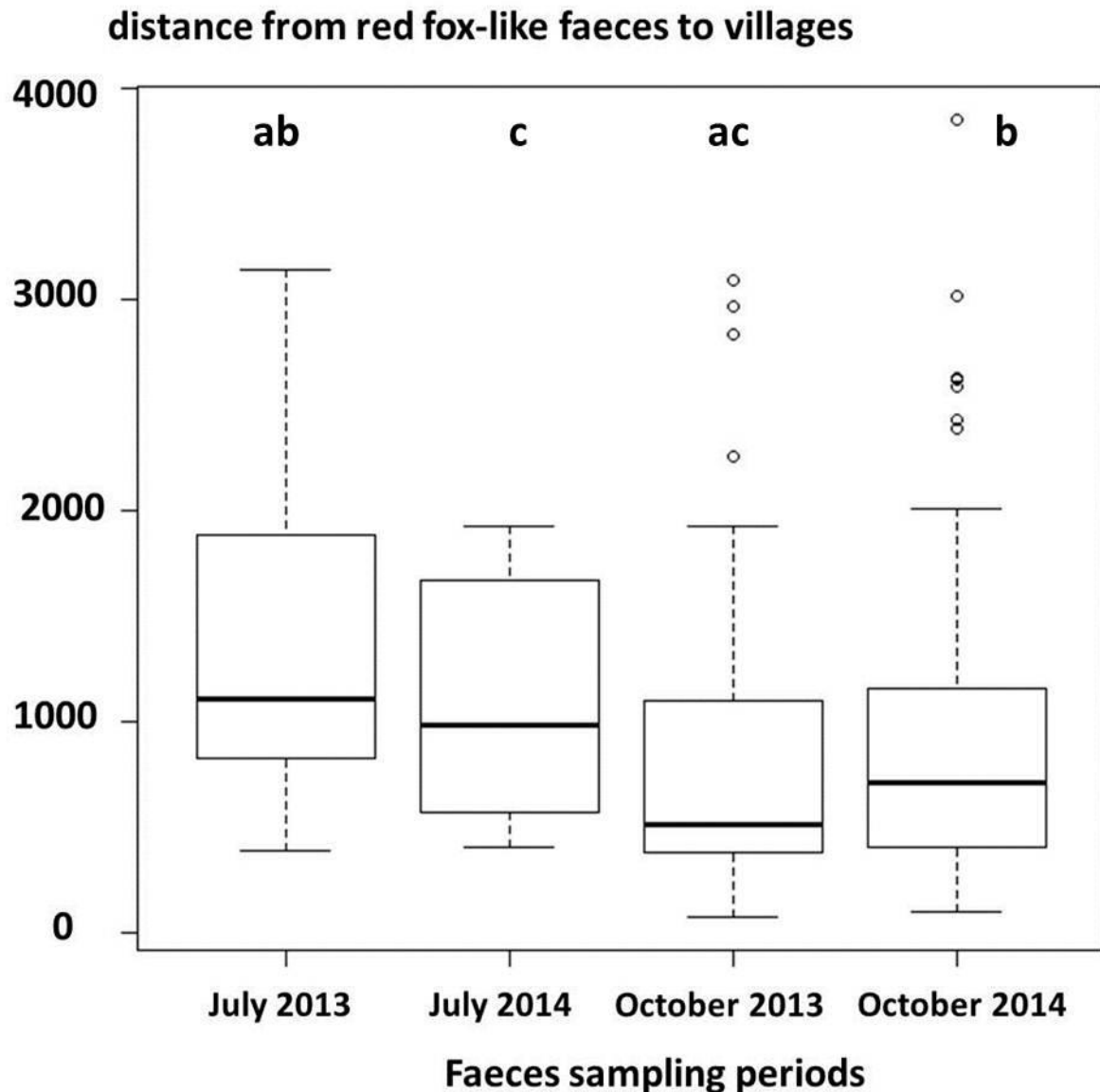


Figure 23 : Distance between red fox-like faeces and villages according to faeces sampling periods (ab: July 2013 vs October 2013; b: July 2013 vs October 2014; ac: July 2014 vs October 2013).

III-3 Red fox diet composition

In average, 24% to 36% of faeces contained undetermined voles corresponding to the period of sampling. In the same time, 0% to 23% of faeces contained *Microtus* spp. and 4% to 7% of faeces contained *A. scherman*. No clear seasonal change in vole occurrence between the summer and the autumn was observed. Insects were one of the most frequent food resources (frequency of occurrence reaching 39% for undetermined arthropods, 38% for orthoptera and 26% for coleoptera (Table 6) with

seasonal consumption for coleoptera (between 22% and 26% during summer and between 6% and 9% in autumn). As a whole, fruits were found in less than 15 % of the scats during summer but could reach 40% of occurrence in autumn. With an occurrence from 10% to 23%, earthworms could be important secondary food resource. Other categories of food resources (mainly birds and meso- or macro-mammals) represent less than 10%. The seasonal pattern of use of this food source was rather constant, with a decrease in summer for undetermined meso- or macro-mammal (Table 6).

Table 6 : Frequency of occurrence of each food item in red fox-like faeces expressed as the percentage of the total number of faeces collected at each site with the presence of the item for each season (between parenthesis the number of positive faeces for each food item category).

Season	Und. arthropod	Orthoptera	Coleoptera	Others	Fruit	Bird	Und. mammal
July 2013	30%(7)	22%(5)	26%(6)	0%(0)	9%(2)	4%(1)	13%(3)
October 2013	39%(42)	38%(41)	6%(7)	< 1%(2)	40%(44)	0%(0)	5%(6)
July 2014	28%(5)	0%(0)	22%(4)	0%(0)	11%(2)	0%(0)	5%(1)
October 2014	33%(33)	22%(22)	9%(9)	0%(0)	27%(27)	3%(3)	3%(3)

Season	Und. Meso/macro- mammal	Und. small mammal	Und. vole	<i>A. scherman</i>	<i>Microtus</i> spp.	Earthworms	
July 2013	4%(1)	4%(1)	30%(7)	4%(1)	0%(0)	13%(3)	
October 2013	11%(12)	4%(5)	24%(25)	6%(7)	6%(7)	24%(25)	
July 2014	5%(1)	11%(2)	28%(5)	5%(1)	5%(1)	11%(2)	
October 2014	10%(10)	5%(5)	36%(36)	7%(7)	23%(23)	10%(10)	

IV - Discussion

IV-1 Spatial distribution of red fox faeces

Giraudoux (1991) has shown that the density of the red fox faeces distribution in the Jura Mountains is much higher in habitats like roads or along hedgerows (faeces KAI per 2 ha reach a 38 times higher value for forested roads than for grassland openfields in April 1990 in Giraudoux (1991)), which represents a very little proportion of the total surface area studied. Grassland areas represent 98% of the total area with thousands of faeces, and the number of fox faeces along roads and hedgerows represents from 3% to 10% of the total number of faeces. During his study, Giraudoux (1991) observed seasonal variations in the number of faeces collected, and that during the winter the number of faeces along roads and hedgerows was higher.

In their study in Alpine context, Patalano and Lovari (1993) and Lucherini and Crema (1994) found that, in winter, frequent snowfalls often prevented faecal collections, both by limiting the movements of foxes and rapidly covering tracks and scats. Moreover, in this study, more faecal samples were found during the summer and the autumn while our results show a 4-5 times higher number of faeces collected in autumn than in summer. In a lower elevation area (Pisa province; from the coast to 980 meters of altitude), Cavallini (1994) showed an opposite pattern of red fox faeces collection with a greater number of collected faeces in spring and summer (1.5 samples per km) than in autumn (< 1 sample per km). One possible explanation given by this author for a lower number of collected faeces in summer than in autumn is a decrease of detectability because of a higher vegetation. He also claimed that a heavy rainfall could wash away faeces and decrease detectability. We also met heavy rainfall every single nights during the first summer of sampling.

We observed statistical differences between distances between faeces and villages with a higher distance in summer than in autumn. Based on field observation, we hypothesize that in autumn (October), weather conditions and changes in some food availability (marmot hibernation, end of livestock presence period, Coleoptera occurrence decrease in diet, first snowfall in altitude) forced the red fox to come back to the lowest part of Haute-Romanche valley, close to inhabited areas. Indeed, Lucherini and Crema (1994) observed that, for example, anthropic food items, such as garbages, were found with higher frequency in faeces in winter.

IV-2 Dietary comparison between Jura and Alps

Giraudoux (1991) showed a grassland vole-dominated diet during grassland vole population outbreak. When the common vole abundance decreased, this species still dominated the red fox diet but its occurrence decreased. The red fox seems to diversify its diet during the low density phase of the common vole in Giraudoux (1991). *Apodemus* spp. and *Myodes* spp. were very little represented except during one summer (during the low density phase of grassland voles, appearance of fruits and insects). Artois and Stahl (1989), in the Lorraine region (eastern France) indicated a slight decrease of the brown hare occurrence in red fox diet when *Microtus* spp. abundance increases, suggesting a potential diet switching of the red fox already mentioned by Ryszkowski (1982) and Goszczynski (1974). However, Giraudoux (1991) did not detect a significant change of lagomorph frequency (2-3%) in the diet during the *M. arvalis* population crash.

Similarly, Raoul et al. (2010) and Jacquot (2013) showed that in the Jura Moutains grassland rodents (*Microtus* spp. and *A. scherman*) contributed substantially in the red fox diet compared to other rodents. Raoul et al. (2010) also showed that in lowland study sites when *A. scherman* was virtually absent from the diet, bird and lagomorph occurrences were higher than in the other sites.

Our data confirm that the red fox can use a large number of potential sources of food present in its habitat such as small mammals (especially voles), insects (mostly Orthoptera), fruits, earthworms, birds or meso/macro mammals (probably lagomorphs and/or marmots). In particular, our results suggest that Orthoptera is an important food resource in elevated Alpine regions. Lucherini and Crema, (1994) in Val Troncea Natural Park (Western Italian Alps) found that the diet of the red fox reflected the montane ecosystems seasonality with a temporal variation of feeding habits determined by food resources availability (Doncaster et al. 1990; Cavallini and Lovari 1991). For example, Lucherini and Crema, (1994) observed that insects and marmots, unavailable in winter, were present almost exclusively in the summer-autumn diet. As we only collected red fox faeces in the summer and autumn we cannot compare our results with these studies, even if environmental conditions and prey phenology are supposed to be similar. Considering large (e.g. lagomorph, etc.) and small (e.g. insects) alternative preys, Weber (1996), in the Jura Moutains, observed that red fox

cubs consumed a higher proportion of large preys (e.g. lagomorph) than adults in the first year of low vole density while small ones (e.g. insects) occurred more the following years. Among the variety of small mammal species available, *A. Scherman* and *Microtus* sp. clearly dominated the red fox diet in our results.

Invertebrates (e.g. insects) can be a rich seasonal food item even in an Alpine habitat (Lucherini and Crema, 1994). In the Cagnacci et al. (2003) study, insects were a seasonally important category, Leinati et al. (1960), instead, did not report the presence of invertebrates in the red fox diet in Gran Paradise area. During the warm season, in the Cagnacci et al. (2003) study, small mammals replaced ungulates in the red fox food habits, possibly because of a drop in carcass availability. These authors claimed that the presence of small mammals in the diet approximately corresponded to their seasonal availability (Delattre et al., 1986) and their difficulties deal with snow cover (Lindström, 1994). As for our results, Cagnacci et al. (2003) claimed that the fruit consumption was seasonally dependent on a greater occurrence during the cold months than in the warm season (Cagnacci et al., 1999).

V - Conclusion

Our results show a 4-5 times larger number of faeces collected in autumn than in summer. In a lower elevation area (Pisa province; from the coast to 980 meters of altitude), Cavallini (1994) showed an opposite pattern. Decrease in detectability because of a higher vegetation in summer or heavy rainfall were considered by Cavallini (1994) as potential sources of fluctuations in the collection of red fox faeces. Furthermore, in our study, fox faeces were found closer to villages in autumn compared to summer. In this study, carried out in a period of low density of *A. terrestris* we confirm that the red fox can use a large number of the potential sources of food in its habitat. In particular, our results suggest that, as could be expected in comparison of Lucherini and Crema et al. (1994), Orthoptera is an important food resource in elevated Alpine regions.

Among the small mammal species available, *A. scherman* and *Microtus* sp. clearly dominated the red fox diet. However, macro-remains did not allow us to identify every prey items in the diet (e.g. Marmot and Lagomorph could not be separated, etc.). It would probably be of interest to use molecular techniques based on the DNA already extracted from each faeces to get more information from our faeces collection.

Chapter III: Variation of predation pressure in a context of cyclic population outbreaks of grassland voles.

Box 3

In this Chapter, we worked in both the Jura Mountains and the Haute-Romanche valley with an experimental approach. We monitored a new alternate prey (meat lures) with camera traps and looked for its consumption in relation with predator species, montane water vole abundance and landscape structure. We recorded predation on 400 meat lures for 5 nights using camera traps in the Jura Mountains (France): 50% of the lures were found by predators after 5 nights; 50% of the observed predators were mammals (mostly red fox but also dog and domestic cat) and 50% birds (mostly corvids). Time to lure discovery was 1.2 times larger for mammals (except cat) than birds. Lure survival was positively correlated to vole abundance but in an extremely noisy context ($R^2 = 0.002$, $p < 0.0001$), as was predator abundance ($R^2 = 0.10$, $p < 0.0001$). Lures were found quicker during vole population increase. Increase in lure survival and in lure consumer abundance during the peak of vole density indicates a prey switching. A positive connection between the NDVI value and the numbers of hours before the discovery of lures was found, advocating for a potential protecting effect of dense vegetation. In the Alpine context, lure survival was positively correlated to vole abundance in an extremely noisy context as in the Jura Mountains. Considering predator species, composition in the Alps was similar to the Jura except for the carrion crow replaced by the northern raven.

A - Introduction

In chapter II, we used different methodological approaches in different areas to study the potential diet switching of the red fox toward alternate food resources. If we evidenced some indication of a possible existence of this diet switching mainly in the Jura Moutains, obviously our analysis brought too fragmented informations with also methodological biases.

Still in those two geographical areas (e.g. Jura Moutains and Haute-Romanche valley), we decided, to develop an experimental study to look for the existence of this diet switching of the generalist predators in cyclic outbreak montane water vole context. A first difference was that we brought in the environment a new alternate food resource. The second was an expansion of the predator species spectrum studied.

By developing a very similar experimental design in both areas, we were given the opportunity to compare our results between our two study areas. To develop this approach, we simultaneously monitored the new alternate food resource consumption and the relative abundance of montane water vole, predator species and other potential preys such as the brown hare.

Chapter III (A): Variation of predation pressure in a context of cyclic population outbreaks of grassland voles: Jura Mountains.

I - Introduction

Worldwide agriculture has undergone large socio-economical and technological changes generally leading to intensification and decreased biodiversity (Loreau et al., 2001; Allen, 2000). Today, in addition to agricultural intensification, specialization is one of the greatest anthropic pressures on biodiversity and ecosystem services (Hole et al., 2005). For example, specialization leads to spatial and technological dissociation between animal husbandry and crop production (Le Roux et al., 2008). While vegetable and crop production is located in the lowlands, farmers in mountainous regions specialized in growing fodder for animal husbandry and milk production (García-Martínez et al., 2011). In this context, mountainous regions are often considered to be more favorable to biodiversity and eco-friendly agricultural practices (Fjeldså et al., 1999). However, even in these areas consequences of husbandry and forestry are significant (Briner et al., 2012).

While some species that depend on agro-ecosystems are declining (Aviron et al., 2009), others are outbreaking according to specific time laps and are considered as agricultural pests (Singleton et al., 2010; Koyanagi et al., 2012; Krebs, 2013). Small mammal pests, including some grassland voles (e.g. the montane water vole (*Arvicola scherman*) and the common vole (*Microtus arvalis*)), have been widely studied with concern about agricultural economy, ecotoxicology, eco-epidemiology and fundamental ecology (Parshad, 1999; Hanski et al., 2001; Zhang et al., 2003; Korpimäki et al., 2004; Giraudoux et al., 2006; Sage et al., 2008; Sluydts et al., 2009; Wang et al., 2010; Decors et al., 2011; Fraschina et al., 2012; Gabriel et al., 2012).

There are many potential drivers of small mammal population outbreaks, and their relative weight is still under debate (Lidicker, 2000). Small mammal populations are characterized by high intrinsic growth rates and strong inter-specific competitiveness (Korpimäki et al., 2004). The biomass production of small mammals could be driven by agricultural intensification and/or specialization, predator guilds modification or weather conditions (Delattre et al., 1996; Delattre et al., 1999; Duhamel et al., 2000;

Stenseth et al., 2003; D'Andrea et al., 2007; Morilhat et al., 2007, 2008; Arlettaz et al., 2010; White, 2011). In temperate Europe and more precisely in the mountainous regions of France, land-use policy led to agricultural specialization of grass production and larger parcels (López-i-Gelats et al., 2011) which promoted multi-annual vole population outbreaks across large spatial and temporal scales and caused populations to geographically spread in traveling waves (Delattre et al., 1992; Giraudoux et al., 1997; Ranta and Kaitala, 1997; Butet and Spitz, 2001; Delattre et al., 2006; Foltête et al., 2008; Berthier et al., 2013) and extremely high crop damages (Spitz, 1968; Grodziński et al., 1977).

In such ecosystems with large multi-annual fluctuations of small mammal abundance, the vole population biomass is a major food resource for predators (Löfgren et al., 1986; Korpimäki, 1989; Hörnfeldt, 2004; Delibes-Mateos et al., 2011; Lanszki and Heltai, 2011). The effects of this resource on food web during multi-annual cycles have been largely documented in European Nordic systems (Hanski et al., 2001; Ekerholm et al., 2004; Gilg et al., 2006). Two kinds of predators are generally considered: specialists whose population dynamics are dependent on a limited number (1-2) of species of small mammals in terms of food (Pellikka et al., 2005; Menyushina et al., 2012), and generalists which could switch their diet and adapt according to the availability of various food resources (Padial et al., 2002; Weber et al., 2002). The functional response of generalist predators can increase predation pressure on alternative prey during the decline of the main prey (Holt, 1977; Hardwood and Obrycki, 2005; Koss and Snyder, 2005; Holt and Huxel, 2007). Several studies bring information on the predation pressure in relation with the type of predators or prey (pest or alternative prey) but only with indirect data (e.g. relation between main and alternative preys) (Leclercq et al., 1997) or in nordic simpler systems (Bêty et al., 2001; Hansson, 2002; Kjellander and Nordström, 2003; Šálek et al., 2004; Broock et al., 2005; Moss et al., 2010; Tornberg et al., 2012). Both indirect data and Nordic systems support the idea that during the decline or the low density phase of small mammals the predation pressure of middle-size predators on younglings or nests of alternative prey increases. Beside, others studies stressed on the potential negative impact of fragmented landscapes versus homogeneous landscapes on the spatio-temporal development of outbreaks of small mammals (Fichet-Calvet et al., 2000; Foltête et al., 2008; Morilhat

et al., 2008) and by extension of the potential protective effect of the landscape on alternative prey.

Mid Altitude Mountains of temperate Europe are more complex than in Nordic systems because of the presence of more diversified landscapes and more diversified food webs. Moreover, the density of montane water vole can reach 1000 individuals per hectare in France, while in Nordic systems density peaks are much lower and rarely exceed some 10 individuals per hectare (Barraquand et al., 2014). A few studies stated that prey switches due to small mammal population decrease may impact populations of game species and/or of conservation concern (Korpimäki and Krebs, 1996; Leclercq et al., 1997; O'Donoghue et al., 1998; Edwards et al., 2000; Weber et al., 2002; Gilg et al., 2006; Delibes-Mateos et al., 2008; Panzacchi et al., 2008; Dupuy et al., 2009; Panek, 2009; Bernard et al., 2010; Morrissette et al., 2010; Raoul et al., 2010; Blanco-Aguir et al., 2012).

The aim of this study is to answer the three following questions: how predators respond to the presence of an alternative prey in a temperate system? Can this response be associated with the variation of small mammal abundance? Is this response influenced by landscape features?

II - Material and methods

II-1 Study site

A 900 km² study area was selected in the Jura Mountains, along the border with Switzerland, in the Doubs (47°10'N, 06°25'E) and the Jura (46°40'N, 05°40'E) departments (Figure 24). The study area elevation ranged between 800 meters in the *Drugeon* river valley and 1463 meters at the *Mont d'Or* top. The study area is characterized by grass production and cattle grazing in open and mixed landscapes and conifer timber production in forested areas. The study area was divided in 500 x 500 m cells. A visual assessment of the abundance of landscape elements was made from the maps of the *Institut Géographique National* (IGN, the French National Geographic Institute) at the 1/25 000 scale and each cell was categorized as 'openfield' or 'mixed' landscape. An open landscape is defined as a grassland openfield while a mixed landscape is defined as a mosaic of grassland hedges and forested areas (Figure 24). Records from the *Fédération de Défense contre les Organismes Nuisibles*

(FREDON), an organisation in charge of controlling vole outbreaks, show that all phases of a small mammal cycle can be encountered in the study area.

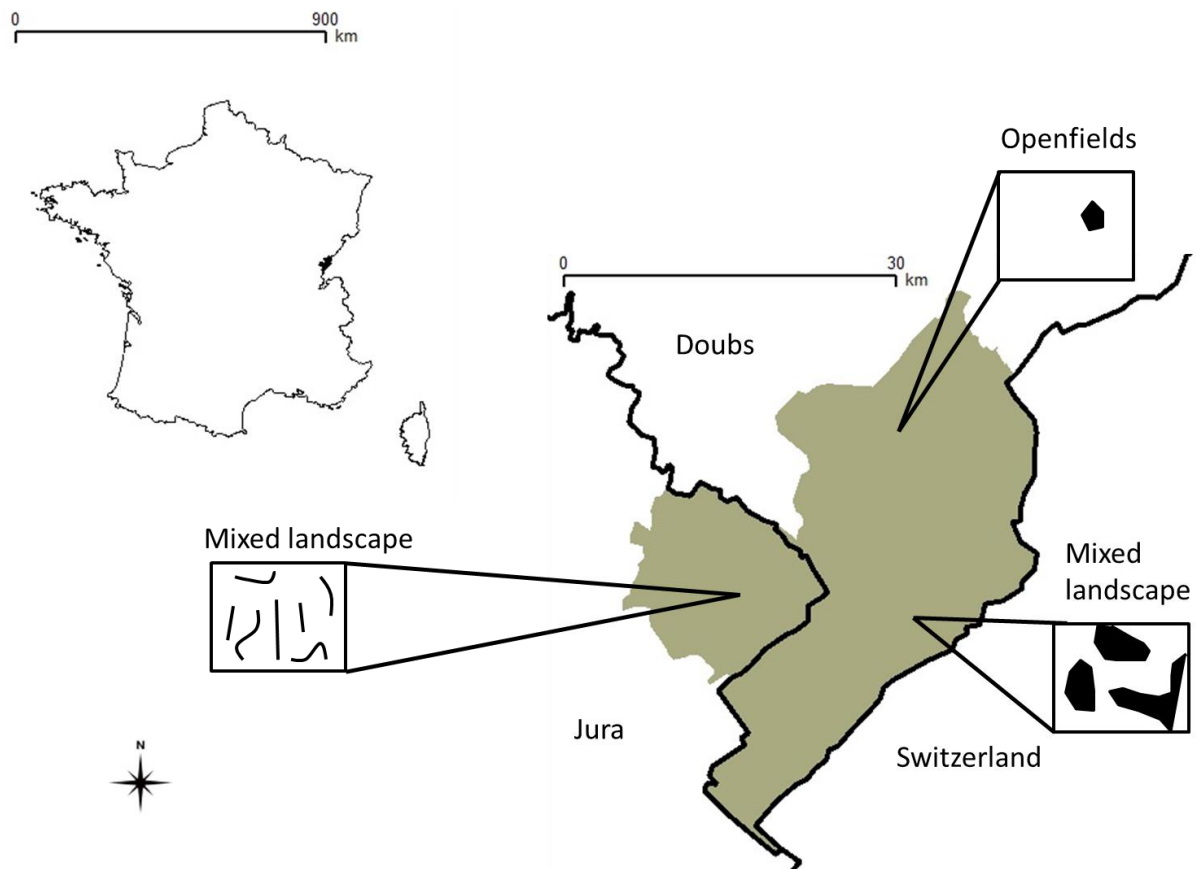


Figure 24 : Location of the study site (in grey).

II-2 Alternate “prey” and preliminary experiments

We used meat lures as alternative prey following Fernex et al. (2011). The lures were designed to draw the attention of predators as much as a leveret would have. The lures were shaped like a sausage made in natural beef skin and filled with pig offcuts. It weighed 180 g and measured 20 cm length for 5 cm large corresponding to the weight of a 2-day-old leveret (Stott and Harris, 2006).

Younglings, such as leverets, have no odor so the sausage skin should guarantee that odor driven predators (red fox, mustelids, etc.) would not be attracted by the scent of the meat. We tested this property in a preliminary quantitative assessment with nine hunting dogs (race : Fox Terrier, West Highland White Terrier, Dachshund, English Setter, Braque Français, Pointer). We hid sausages with three different skins (plastic, beef gut and pig gut) close to a fix element of the landscape (bushes, hedgerow, etc.)

and measured the distance from which each dog detected the sausage by pointing the localisation of the lure. Differences were statistically tested using a mixed effect linear model with the distance as response variable, the sausage category as independent variable and the dog as random variable. According to the results, we chose to use the beef gut which present the lower distance of detection among natural guts.

A pole was necessary to set up a camera trap at a 1m distance from each sausage. We tested the effect (if any) of the presence of pole on lures discovery by using 25 lures with poles and 25 lures without poles and monitored the time of discovery by aerial predators (crows, raptors, etc.) between the categories. Statistical analysis used a parametric model of survival analysis. The aim of this model was to determine and compare the mean time of discovery of the lures (Y) for the two categories of the variable stacks (with and without) as a function of the time of discovery (t). We applied an Age-Specific Hazard Models with a Weibull distribution which correspond to an exponential evolution of the hazard (risk of lure discovery) regardless to the time (Siler, 1979; Crawley, 2007; Fieberg and DelGiudice, 2011). This assumes a constant hazard (a) due to time-independent accidents. The shape parameter of the model is represented by λ . Our model is defined by the following equation:

$$Y = a \lambda (\lambda t)^{a-1}$$

Finally, we accounted the potential effect of the disappearance of a lure on the potential fluctuation of the time before the discovery of the next lures. We tested this property in a preliminary quantitative assessment by comparing the time of the discovery between each lures with the number of meat lures remaining available after each discovery. Differences were statistically tested using a mixed effect linear model with the time before discovery between each lures as response variable, the number of lures remaining as independent variable and time as random variable.

II-3 Experimental design

Each sampling unit consisted in a camera trap placed nearby a fixed element of landscape and facing the meat lure (1 m) (Glen et al., 2013).

400 locations were selected in order to represent a balanced sampling between the 4 phases of a population outbreak (increase, outbreak, decline, low abundance) and the

2 landscape contexts (openfield, mixed). This totalled 8 different situations. The 8x50 locations were randomly selected in the 500x500 m grid.

From May 1st to July 14th 2013 we positioned 50 sampling unit per week for 10 weeks (400 at the end (Figure 25a)). We used latex gloves to minimize lure impregnation with human smell. The installation of sampling unit was achieved at night in order to prevent direct observation from diurnal predators, such as crows (Madden et al., 2015). Each camera trap was set in place for 5 nights and 5 days.

A lure was considered “found by a predator” if eaten, moved or if we got photographic evidence of a predator paying attention to it (smelling, observational posture, etc.). In these cases, the camera trap enables to monitor the predator species and the time of discovery (Comte et al., 2013).

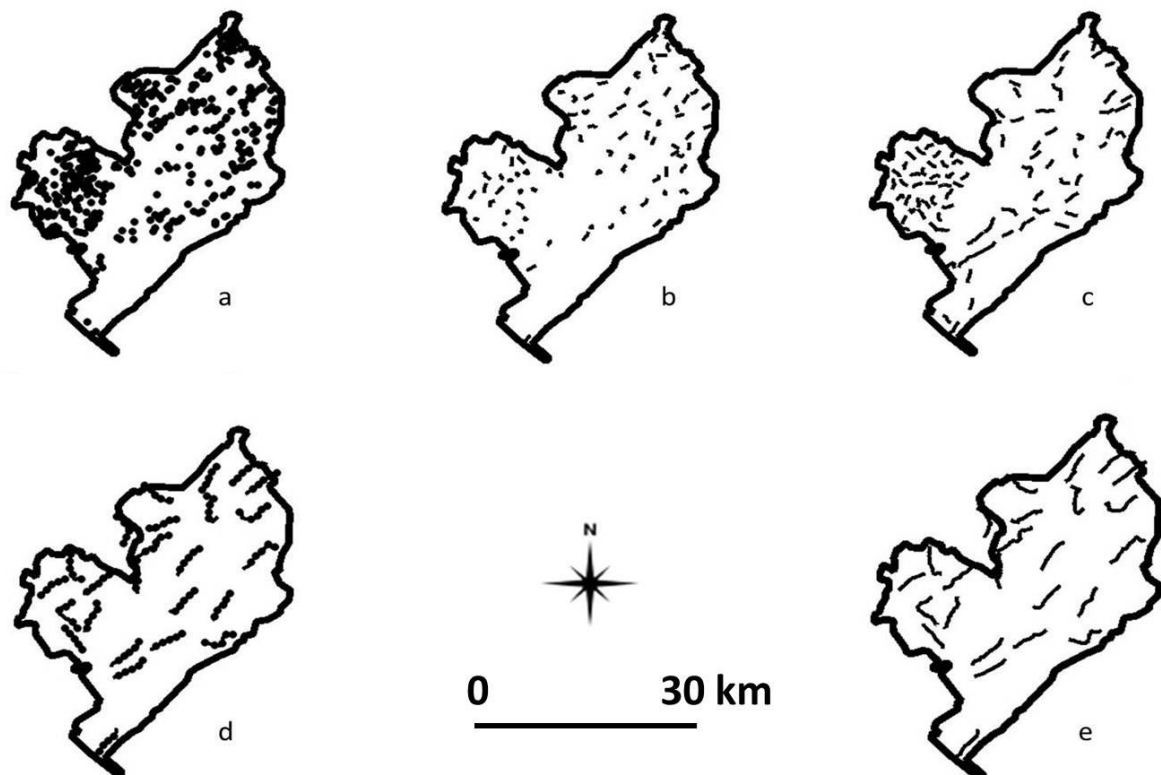


Figure 25 : Organization of wildlife survey: meat lures (a), small mammals (b), night counting (c), diurnal bird survey (ACT (d) and bird of prey (e)).

II-4 Montane vole monitoring

Small mammals (montane water vole (*Arvicola scherman*), European mole (*Talpa europaea*), common/field vole (*Microtus* spp.)) relative abundance was estimated using methods derived from Delattre et al. (1990), Giraudoux et al. (1995) and Quéré et al. (2000). A total number of 81 transects were walked to the study site (Figure 25b). Each 1000 m transect were subdivided into 10 meters' intervals with an observational strip of 5-meter width. The presence or absence of small mammals was recorded for each. An interval positive for vole presence is an interval with at least one surface index (earth tumulus or vole hole). The relative abundance of small mammals was calculated as the ratio of the number of positive intervals divided by the total number of intervals (Duhamel et al., 2000; Raoul et al., 2001; Morilhat et al., 2008; Raoul et al., 2010).

Our measurement of montane water vole relative abundance alone did not allow us to determine the population cycle phase at a given place (e.g. low density, increase, peak and decrease phase). In order to allocate relevant locations to camera we needed the vole cycle history. This was provided by a commune scale FREDON survey carried out each year since 1989. Here, vole abundance was scored at the commune scale (mean area = 9km²) according to the following categories: 0 =no colony, 1=some isolated colonies, 2 =colonies present in many grasslands, 3=very numerous colonies and serious damages to grassland (Berthier et al., 2013). The advantage of this method was to provide a long-term history of the vole cycle.

Figure 26 shows the decision tree used to categorize each combination of relative densities and FREDON population cycle phase in order to allocate a phase to each camera trap. To discriminate decline and increase phase we looked for both relative abundance and cycle phases during the previous autumn (outbreak or low density). To determine the limit between two outbreak phases, we used thresholds given by Chabalier et al., 2009 in Delattre and Giraudoux, 2009 based on a comparison between montane water vole trapping data and the method developed by Giraudoux et al. (1995). This indicated that in rich meadows, the threshold for outbreak phase is situated at about 200-250 ind/ha in spring or summer corresponding to 40% of positive intervals in Chabalier et al., 2009 in Delattre and Giraudoux, 2009. We decided to use these thresholds, even if they were calibrated in Auvergne, because of the absence of calibrated thresholds published or known in the Jura Mountains.

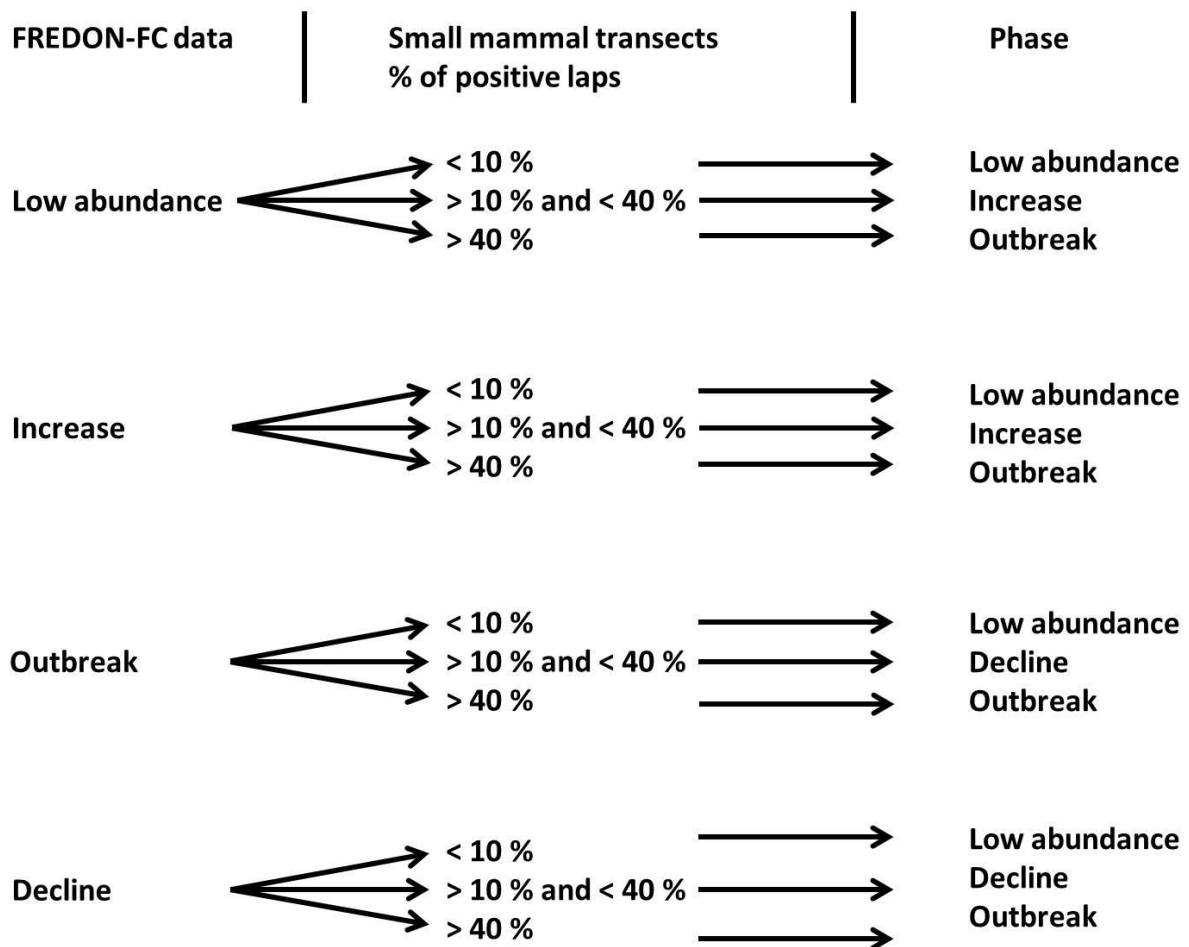


Figure 26 : Decision tree to allocate a phase of the montane water vole outbreak to a camera trap.

II-5 Small mammal relative abundance interpolation

The potential connectivity between patches of grassland habitat of montane water vole is generally limited by forested areas (Berthier et al., 2013). Therefore, we divided our study area in three sub-areas and checked the absence of spatial autocorrelation. A trend surface was computed separately in each area:

(1) The area located in the Jura department (Figure 24) corresponding in the north to openfields and in the south to mixed landscape,

(2) An area at the North-East of the study area in the Doubs department (Figure 24) characterized by openfields and some little mixed landscape patches,

(3) A third area located in the Doubs department near the Switzerland (Figure 24),

characterized by a mosaic between openfields and mixed landscapes.

II-6 Wildlife monitoring

Brown hares (*Lepus europaeus*), red foxes (*Vulpes vulpes*) and badgers (*Meles meles*) were monitored using night road side counts to estimate their relative abundance (Reynolds and Tapper, 1995; Ruelle et al., 2003; Parrott et al., 2012). Monitoring was performed for 3 nights from April to May 2013 along 87 geo-referenced 1-2 km transects (Figure 25c). Counts were performed at least 1 h after sunset in a car (maximum speed 20 km/h and by 4 people: a driver, a data recorder and 2 observers) using a 100 W spotlights and binoculars for species identification. Double counting was unlikely because transects were relatively straight and observers were careful about animal movements. A Kilometric Abundance Index (KAI) was calculated for each species and each transect as the maximum number of animals from one species recorded by kilometer, providing a lower limit for the minimal number of individuals of this species.

Alaudidae, *Turdidae*, *Phasianidae*, *Colombidae* and *Corvidae* were monitored using the Ponctual Abundance Index method (Roux et al., 2012). Along 5 km transects (n = 25 transects (Figure 25d)) 5 monitoring spot were placed. At each spot, the observer registers the number of each species by listening and watching in a circle of a 500-meter radius (number of individuals per point).

For diurnal raptors, monitoring was conducted along the same 5 km transects (n=25 (Figure 25e)) driven by car between 6 and 11 AM with only one repetition (Fuller and Mosher, 1981; Viñuela, 1997; Boano and Toffoli, 2002; Møller and Mousseau, 2009; Vergara, 2010). The relative abundance is the KAI.

No method was available for the monitoring of mustelids at large scale resolution (Erlinge, 1974; King, 1975).

II-7 Characterization of landscape context

Firstly we characterized the landscape structure with the qualitative classification used to define the sampling of the experiment as “openfield” or “mixed” landscape. Secondly, we used the normalized difference vegetation index (NDVI) in order to obtain a relative index of vegetation biomass (Martinuzzi et al., 2008). An increase of the NDVI value generally reflects an increase of vegetation biomass. We chose remotely sensed data at 30 m spatial resolution because it enables land cover to be mapped over a very large area. Satellite data was acquired in June 2013, by Landsat 7 ETM. NDVI is defined as (Rouse et al., 1974; Valor and Caselles, 1996):

$$NDVI = \frac{(NIR - VIS)}{(NIR + VIS)}$$

where VIS and NIR stand for the spectral reflectance measurements acquired in the visible (red) and near-infrared regions, respectively. NDVI was computed by circle buffer from the location of each camera trap of 500 m radius.

II-8 Spatial interpolation of montane water vole and total predator relative abundance

Montane water vole, predator abundances and camera trap results being not collected on the same sampling grid, interpolation on a common grid was necessary. We have chosen to use a General Additive Model (GAM) to compute a trend surface of montane water vole and predator relative abundance with the same methodology presented in Chapter II-A.

Correlations between our two response variables (time before lures discovery and predator relative abundance) and our independent variable (montane water vole abundance) were computed at 500-meter radius buffer centered on each camera trap resolution over the whole study area. Therefore, each experimental camera trap device was associated with an interpolated montane water vole index and an interpolated predator index.

II-9 Statistical analysis

(1) In order to test whether there is a statistical difference between the variation of the lures discovery time according to the type of predators, the type of landscape structure, the week of experiment or the phase of the cycle, we computed an Age-Specific Hazard Models with a Weibull distribution with regards to previously cited parameters. We applied an Age-Specific Hazard Models with a Weibull distribution which correspond to an exponential evolution of the hazard (risk of lure discovery) regardless to the time (Siler, 1979; Crawley, 2007; Fieberg and DelGiudice, 2011). This assumes a constant hazard (a) due to time-independent accidents.

(2) In order to test if there is a statistical difference between the lures discovery time according to the GAM-modeled relative abundance of montane water vole and the NDVI value we used General Linear models (GLM) following a Poisson distribution as already presented in Chapter II-B).

(3) In order to test whether there is a statistical difference between the GAM-modeled relative abundance of total predators and the GAM-modeled relative abundance of montane water vole, we computed a simple linear model after checking the normal distribution of residual variation (Kolmogorov-Smirnov Test (Kolmogorov, 1933; Smirnov, 1948)) and visually the homocedasticity of the variance.

II-10 Computing environment

Spatial analysis and GIS data management were performed using Quantum GIS 1.8.0-Lisboa (Quantum Gis, 2013), GRASS GIS 6.4.2 (Grass Development Team, 2012) and R 2.15.1 (R-Core Team, 2012b) using the packages car (Fow and Weisburg, 2011), foreign (R-Core Team, 2012a), maptools (Lewin-Koh et al., 2012), mgcv (Wood, 2011), pgirmess (Giraudoux, 2012), raster (Hijmans and Van Etten, 2012), rgdal (Keitt et al., 2012), rgeos (Bivand and Rundel, 2012), Rlab (Boos and Nychka, 2012), sp (Bivand et al., 2008).

III - Results

III-1 Alternate “prey” and preliminary experiments

III-1-a Lure design

No statistically significant difference was found in discovery distance between plastic and beef gut (Table 7). Both of them were detected at significantly shorter distance compared to the pig gut (Table 7). We failed to detect statistical difference of mean time (Y) of lure discovery between with or without pole presence (Table 7).

Table 7 : Results of preliminary experiments about gut type, stacks presence and disappearance of lures.

Relation tested	Model used	Distance of detection	P-value (0.05)
Plastic vs beef gut	mixed effect linear model	0.25 m < mean distance < 2 m	0.21
Plastic vs pig gut	mixed effect linear model	mean distance = 4.75 m	0.003
Beef vs pig gut	mixed effect linear model	mean distance = 4.75 m	0.04
With vs without stacks	Age-Specific Hazard Models	-	0.13
Time to lure discovery after disappearance of the previous one	mixed effect linear model	-	0.08

III-1-b Preliminary verification

We cannot prove a positive or negative effect of the discovery of a lure on the time before the discovery of the next one (Table 7). We tried to see if the period of the lure deposition impacts lure survival. It appeared that weeks from 7th to 10th present better lure survival than during the 1st to the 6th weeks (Age-Specific Hazard Model, $0.007 < P\text{-value} \leq 0.05$).

III-2 Predator guild composition

Approximately half of the meat lures were consumed (48%) after 5 days. Within these 48% of consumed meat lures, red fox is the main predator (26% of the meat lures consumed) close to corvids (25%) (carrion crow (13%), Eurasian magpie (*Pica pica*)).

(7%), Eurasian jay (*Garrulus glandarius*) (1%), northern raven (*Corvus corax*) (3%) and undetermined corvids (1%)) and domestic animals (20%: 10% for dog (*Canis lupus domesticus*) and 10% for cat (*Felis catus catus*)). Others predators had been observed as un-identified predators (11%), European badger (5%), common buzzard (*Buteo buteo*) (7%), red kite (*Milvus milvus*) (3%), polecat (*Martes putorius*) (0.5%), wild boar (*Sus scrofa*) (0.5%) and undetermined *Martes* spp. (2%)).

III-3 Landscape and vegetation biomass

We failed to detect an effect of the landscape category (“openfield”, “mixed landscape”) on the mean value of time of discovery of lures (Age-Specific Hazard Model, P-value = 0.13) while it exists a linear and positive correlation (ANOVA, p-value < 0.0001; $R^2 = 0.02$) between the numbers of hours before the lure discovery and the NDVI value (Figure 27).

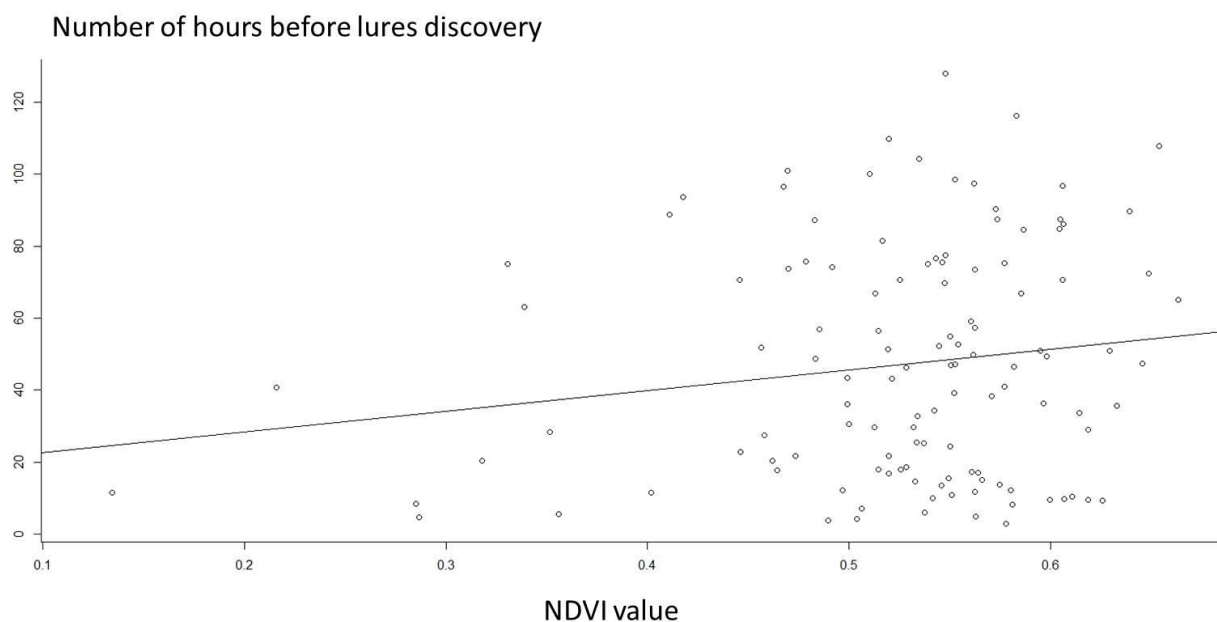


Figure 27 : Number of hours before lures discovery regard on NDVI value.

III-4 Montane water vole abundance and population cycle phases

We found a positive correlation between the time needed for a predator to find the meat lure and the relative abundance of the montane water vole. (ANOVA, p-value < 0.0001; $R^2 = 0.002$). The higher the abundance of montane water vole, the higher the time needed for a predator to find the meat lure.

Moreover, the mean time of lure discovery was significantly shorter during the density increase phase (mean time = 143 ± 1.16 hours) compared to the decline phase (mean time = 230 ± 1.25 hours) and low density phase (mean time = 285 ± 1.22 hours) of the montane water vole cycle (Age-Specific Hazard Model, $0.003 < P\text{-value} < 0.0004$) (Figure 28). Considering the high density phase of the vole cycle, the chosen threshold did not allow us to keep this category in the survival analysis.

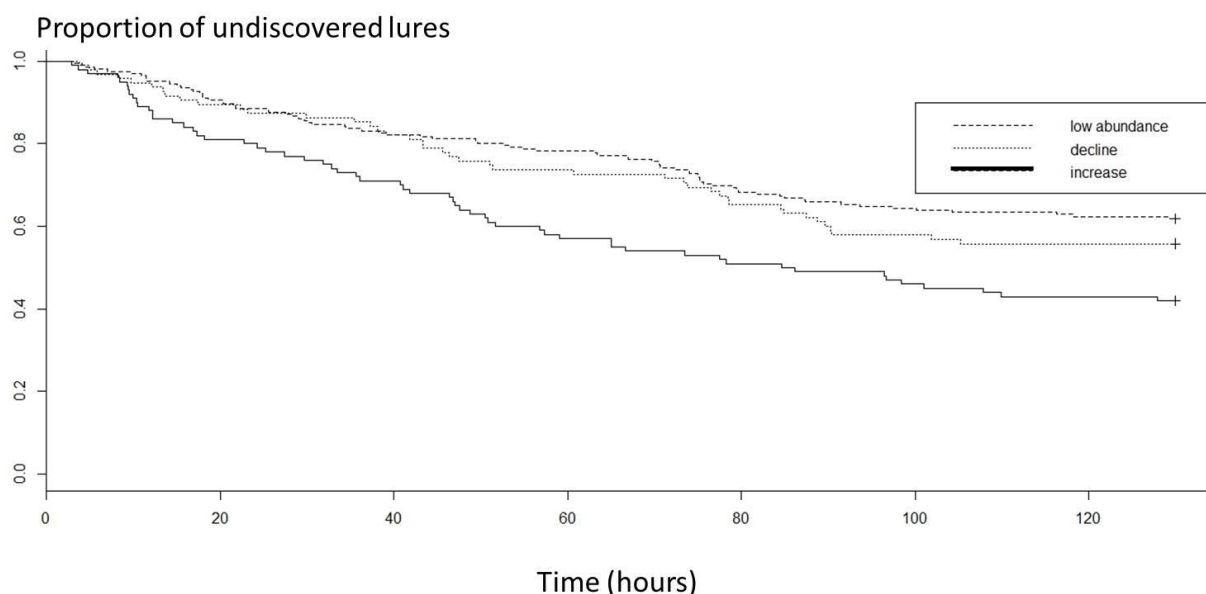


Figure 28 : Proportion of undiscovered lures during time (hours) regard on phases of the montane water vole outbreak.

III-5 Response of predators to the presence of the montane water vole and the lures

We found linear and positive relationships between the relative abundance of montane water vole and the relative abundance of red fox, carrion crow and red kite during the decline phase and a negative one for the fox during increase phase (ANOVA, $0.1 < p\text{-value} < 0.0001$; $0.04 < R^2 < 0.22$) (Figure 29a, 29b, 29c). Conversely we failed to detect a relationship between the relative abundance of montane water vole and other predators.

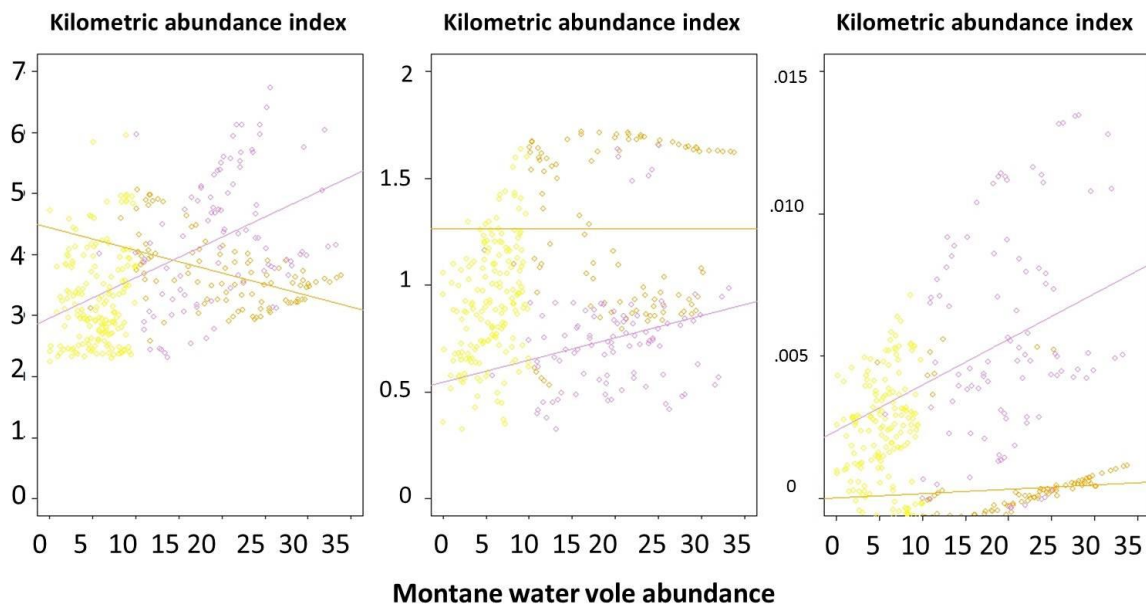


Figure 29 : Gam-modeled relative abundance of (a) red fox, (b) carrion crow , (c) red kite regard on GAM-modeled relative abundance of montane water vole according to phases (low abundance (yellow), increase (orange) and decline (purple)).

Figure 30 shows that the mean value of time of discovery of the lures was significantly larger for the domestic dog and the badger (mean time = 71 ± 1.23 hours) than for the domestic cat (mean time = 41 ± 1.29 hours), the carrion crow (mean time = 41 ± 1.28 hours), the red kite (mean time = 37 ± 1.38 hours) and the Eurasian magpie (mean time = 40 ± 1.31 hours) (Age-Specific Hazard Model, $0.02 < P\text{-value} < 0.04$) (Figure 30a, 30c, 30d, 30e, 30h and 30i respectively). This phenomenon is the same for the red fox (mean time = 59 ± 1.25 hours) which present a mean value of time of discovery of the lures significantly larger than for domestic cat, carrion crow and Eurasian magpie (Figure 30a, 30c, 30d, 30e and 30i).

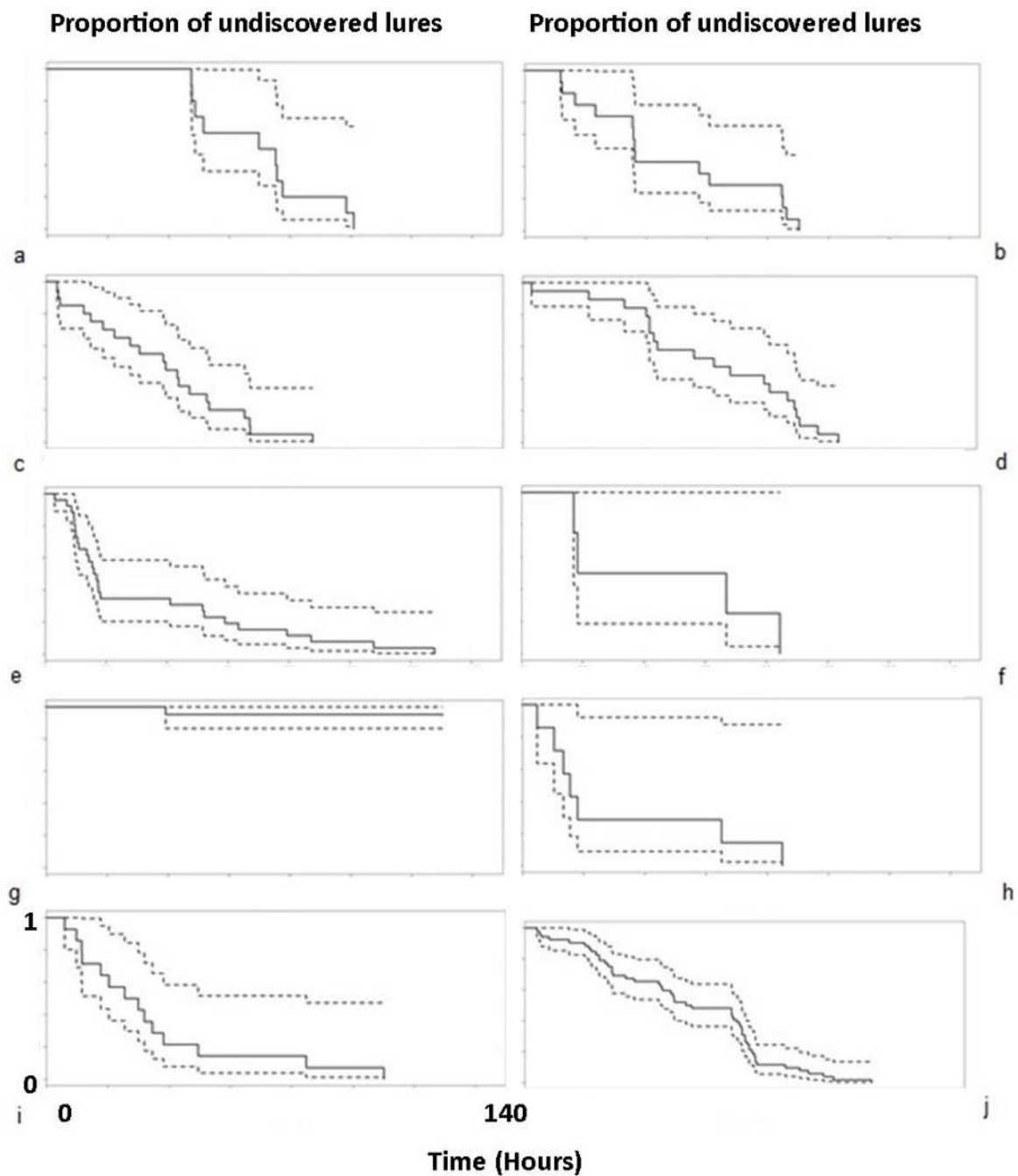


Figure 30 : Proportion of undiscovered lures during time (hours) regard on predators: a (badger), b (common buzzard (*Buteo buteo*)), c (domestic cat (*Felis catus catus*)), d (domestic dog (*Lupus canis domesticus*)), e (carrion crow (*Corvus corone corone*)), f (northern raven (*Corvus corax*)), g (undetermined predators), h (red kite (*Milvus milvus*)), i (Eurasian magpie (*Pica pica*)), j (red fox).

III-6 Importance of the day-time period in the lure discovery

Lure ratio discovery is a linear progression through time (Figure 31). There are no differences in the ratio between day or night with a mean value of 0.29 and 0.24 respectively (ANOVA, p-value = 0.12; $R^2 = 0.02$ - Figure 32).

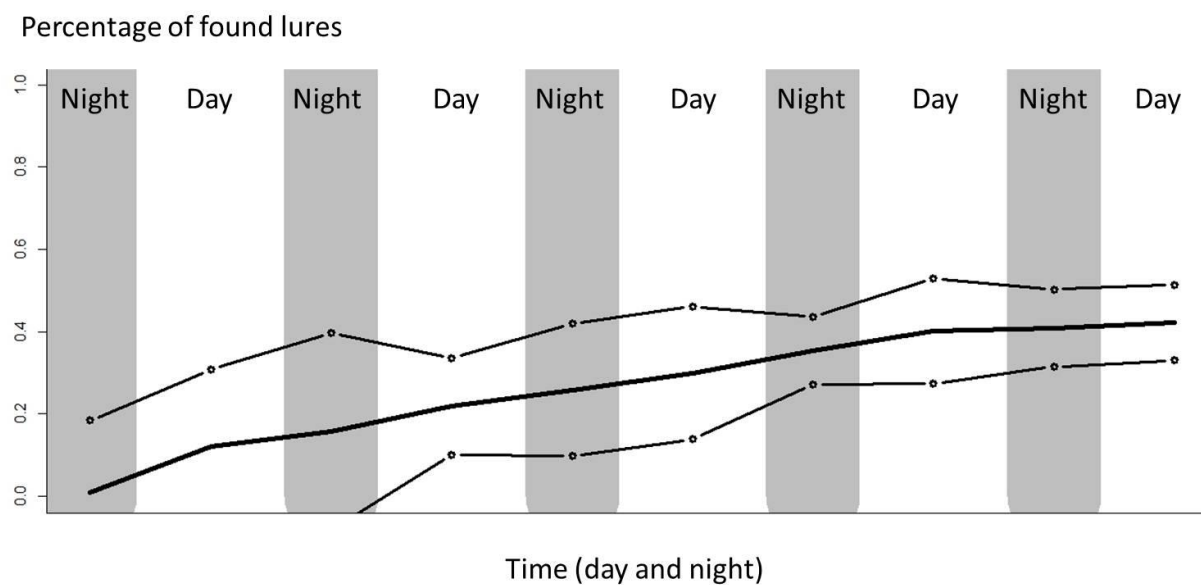


Figure 31 : Dynamic of lure discovery with time, divided by day and night periods.

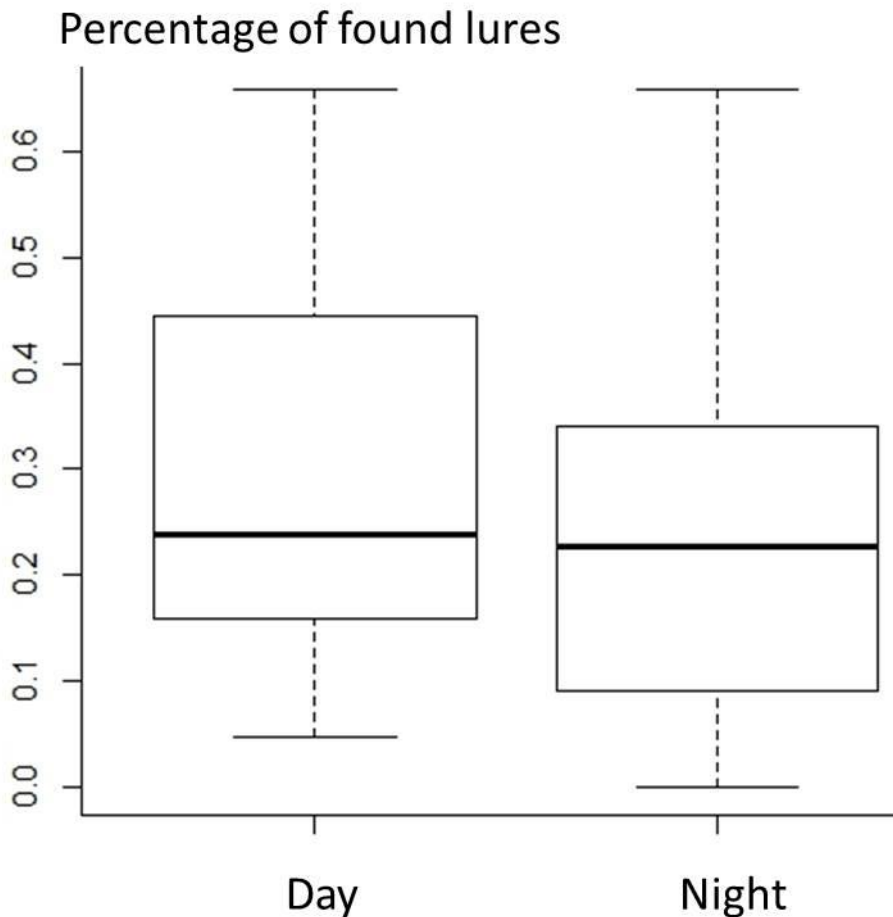


Figure 32 : Comparison of lure discovery divided by day and night periods.

IV - Discussion

IV-1 Statistical relationships but noisy context

We found statistical relationships between variables but the percentage of explained variance was generally very low (often less than 10%). Schaffer (1985) pointed out that considering a “simple” relationship between the population dynamic of a single species with one variable might be an error because a species under study has to be considered in its entire complex ecosystem. McCann and Yodzis (1994) observed that the more a food chain is complex the more the system will be chaotic and the more it will be difficult to isolate a “simple” ecological process from the entire system. Considering that our study area is located in a temperate ecosystem with complex food chains (many predators, many preys and many kinds of habitats in various landscapes) it is likely that many ecological drivers interfering in such system escaped investigation and contribute to the noise recorded. Considering that our results show weak

correlations, one must relativize the following discussion and conclusion as not definitive at all. Limited in this work by our capacity (knowledge and time shortage) to applied more robust mathematical analysis (e.g. comparing the results obtained to those obtained with other approaches such Bayesian's simulation based on processes, etc.), this exploratory analysis obviously paves the way to complementary investigations on the dataset.

IV-2 Composition of predator guild

In our study, the proportion of predators, consuming the meat lures, was slightly larger for mammals than avian predators (50% and 40% respectively). A number of studies have dealt with scavenging on carcasses (Sullivan 1988; Tobin and Dolbeer, 1990; Linz et al., 1997; Travaini et al., 1998; Prosser et al., 2008). The rare ones dealing with camera trapping on carcasses mention both terrestrial and birds scavengers (Kostecke et al., 2001; DeVault et al., 2003; Jennelle et al., 2009; Villegas-Patraca et al., 2012). In these studies, the proportion of scavengers is greater for mammals than for birds (80% vs 20%) excepted for Travaini et al. (1998) who observed more bird (87.5%) than mammal scavengers (12.5%) and Montaz et al. (2014) (more than 66% of carcasses consumption by birds). However these last authors only observed during daytime only, and probably missed nocturnal consumption, which may underestimate the presence of mammals. Our results are very close to those obtained by Fernex et al. (2011), who used the same methodology as us and show a predator guild composition feeding on the alternate food resource available of 53% of mammals and 47% of birds especially crows.

IV-3 Sources of lure consumption variability

At the end of the experiment, about 48% of the lures were found by a predator. Literature shows that - rates of consumption of carcasses are very variable. Indeed, in some studies after only one day on field about 42% (15% for us) of carcasses remained consumed (Linz et al., 1997) and 94% (22% for us) after two days (Travaini et al., 1998) which is much faster than in our study.

This could be explained by the difference of habitats: Woodlots and crops fields for Linz et al. (1997) and steep rugged valleys and large rivers for Travaini et al. (1998)'s.

In Travaini et al. (1998) example, main carcasses consumers were considered as “true” scavengers or as very efficient carcasse consumers with species as chimango caracara (*Milvago chimango*), northern crested caracara (*Caracara cheriway*), black vulture (*Coragyps atratus*). For four days of field exposure between 13 and 91% carcasses were found (Tobin and Dolbeer, 1990; DeVault et al., 2003; Prosser et al., 2008). Indeed, firstly, in the Jura Mountains excepting the red kite and black kite the observed and non-observed predators do not included “true” scavengers or very efficient carcasse consumers. This observation could be a first explanation of a better lure survival in our study area compared to other studies.

Authors cited below argued that this great variability could be first explained by seasonality. Seasonal variations in scavenger activity and seasonal variation in carcasse decomposition could account for the different survival times for carcasses (Tobin and Dolbeer, 1990). Although animal deaths due for example to repetitive time process as seasonality could provide seasonal pulses of carcasse availability. For example, large-scale die-offs of salmon cohorts produce an abundance of carcasses at regularly spaced intervals (Hewson, 1995, Ben-David et al., 1997). Another example is that in temperate areas, bad weather conditions such as snow during winter or an increase in predation rate could lead to starvation (Clevenger et al., 1992; Huggard, 1993; Green et al., 1997) and then an increase in death of some animals with again an increase in carcasse availability. Some facultative scavengers may increase their reliance on scavenging during these predictable time periods (Wilton, 1986, Huggard, 1993).

It could be also explained by world scale localization of the study site. Houston (1985)’s studies showed that Neotropical forests provide a greater food supply to vertebrate scavengers than Afrotropical forests due to the higher biomass and smaller average size of herbivorous mammals in Neotropical forests. Then, carcasses remain available to vertebrates in Neotropical forests for longer periods than in Afrotropical forests. This author explained that fly larvae completely consume 2–10 kg carcasses within three days in Afrotropical forests, whereas in Neotropical forests, ant community extending the availability of carcasses to vertebrates to over 10 days (Houston, 1985). Invertebrate community could influence the number and type of carcasses available to vertebrates. For instance, burying beetles (genus *Nicrophorus*; around 75 species)

which we observed during our experiment are found throughout the northern hemisphere. *Nicrophorus* beetles are obligate carrion breeders – and could make disappeared quickly small carrion (Milne and Milne, 1976). However, in this region *Nicrophorus* beetles are active only during the warm season when they compete with other insects and vertebrates for small carrion items (Smith and Merrick, 2001). All these potential factors explain both the great variability of the carrion remaining in the studies we cited and that it's very difficult to compare the time to lure discovery with others carrion studies over the world.

Another potential explanation is based on the great importance taken by grassland voles for predators in our study area. Indeed, more than twenty predator species feed on voles (Lachat Feller, 1993; Berny et al., 1997; Michelat and Giraudoux, 1999, 2000; Schmidt et al., 2002; Weber et al., 2002; Russell and Storch, 2004; Dell'Arte et al., 2007; Roulin et al., 2008; Delattre and Giraudoux, 2009; Bernard et al., 2010; Bayle and Schauls, 2011; Lefranc and Paul, 2011; Quéré and Le Louarn, 2011; Tschanz et al., 2011; Coeurdassier et al., 2012; Savouré-Soubelet et al., 2012). Considering that vole biomass is probably one the most important food resource for predators in the Jura Mountains, it could explain why predators use our lures as alternate food resource very secondarily.

IV-4 Response of predators to the presence of the lures and landscape effect

In our study it appears that avian predators (carrion crow, Eurasian magpie, red kite) found the lures faster than terrestrial predators (domestic dog, red fox or badger). Birds are best at looking for the lures because of their capacity to search large area at low energy cost with soaring locomotion compared to the running locomotion of mammal predators (DeVaut et al., 2003).

Fernex et al. (2011) showed that the difference of lure survival on the edge was smaller than in the middle of the fields. They hypothesized that predation increases with the proximity to a habitat discontinuity, or an edge between two habitats (Gates and Gysel, 1978; Yahner, 1988). The first evidence for this phenomenon was presented by Gates and Gysel (1978) who found support with observational data from passerines in three study sites in Michigan. The notion of an "edge effect" had been suggested earlier by

Leopold (1933). Together with the concept that predation is density dependent (Krebs, 1971; Fretwell, 1972; Dunn, 1977), Gates and Gysel (1978) suggested that habitat edges may function as ecological traps for preys.

Here no effect of landscape categories was detected and we used NDVI as an indirect measure of vegetation biomass here assume to be a difference between “simple” grassland and grassland with edges (bushes and trees). We show that the larger the vegetation biomass in a buffer of 500 m radius around a lure, the larger the lure survival. In this case, higher and denser vegetation would protect or hide the lure against predators. For example, particularly during the spring, brown hares need habitat structures that provide more cover from predators and from unfavourable weather conditions (Jennings et al., 2006; Pépin and Angibault, 2007).

Another result is the presence of a positive effect of the time on the survival of the lures: lures are still less likely to be found from week 7 to 10 than from week 1 to 6. The 7th week of the experiment corresponded to the main period of mowing with agricultural machine and an increased presence of human. Indeed, Yasué (2005) showed that, according to optimal foraging theory, animals will decide where and how to feed based on a trade-off between starvation and predation risks (Krebs and Davies, 1987; Lima and Dill, 1990; Lima, 1998). Shorebirds apparently perceive humans as predators (Frid and Dill, 2002). Consequently, when people are present, they may attempt to decrease “predation” risk by spending more time scanning for approaching humans (Burger and Gochfeld, 1991; Fitzpatrick and Bouchez, 1998; Thomas et al., 2003). Another potential factor could be that just after mowing with modern agricultural machine, there is no longer high grass protection for rodents and predation on rodents is therefore facilitated with a decrease of predation on alternative food resources.

IV-5 Diet switching hypothesis

Previous studies showed that in a context of cyclic outbreaks of small mammals with diet switching, there is a positive relation between the abundance of the small mammal and the alternative prey (Leclercq et al., 1997; Saniga, 2002; Tornberg et al., 2012). However, this could not have been shown in our study area using dietary analysis of fox faeces. Indeed, during a 3 years’ diet analysis including a decline in abundance of

common vole (*Microtus arvalis*), Giraudoux et al. (2002) showed that remains of brown hare represent 3% of the diet and they could not find a statistical difference of this proportion before and after the decline of the common vole. However, the very low density of brown hare in the Doubs and Jura Department could explain this absence of diet difference for brown hare. Conversely, by studying diet composition in red fox den during reproduction period, Panek (2009) confirmed a positive effect of larger abundance of brown hare on the proportion of adult hare remains in a den and he found a significative and negative impact of vole abundance on the proportion of adult remains in a den in a 9 years' survey. This study confirms results obtained by Goszczyński and Wasilewski (1992) who showed that in spring the consumption of hare by foxes was the highest throughout a whole year coinciding with seasonally low vole densities (Goszczyński, 1977). Moreover, Soviš (1967) and Kožena (1988) in Czecho-Slovakia also indicated the importance of hare in fox diet in spring. The presence of young hares in spring more vulnerable to fox predation may also raise the consumption of this species.

Our results show a significant statistical link between a high relative abundance of montane water vole and a longer time of survival of the lures. This may be considered as an indication of a diet switching, whose consequences on focal prey species is still to explore

IV-6 Response of montane water vole predator abundance to the presence of vole

During the increase phase of montane water vole cycle the lures were found faster than in low abundance or decline phases. Cornulier et al. (2013) and Millon et al. (2014) pointed out the dampening of Microtine population cycles in Europe, since the mid 80s. Before this period, in Fennoscandia, northern small mammals formed a gradient from non-cyclic in southern Sweden (Erlinge et al., 1983) to cyclic vole populations in western Finland (Korpimäki and Norrdahl 1989, 1991a, 1991b) to strongly cyclic populations in northern Fennoscandia (Henttonen et al., 1985). Many researchers have commented on how prey cyclicity is more pronounced in northern regions, and Hanski et al. (1991) have suggested that generalist predators in southern Scandinavian areas dampen cycles created by specialist predators. The study by

Erlinge et al. (1983) of voles in southern Sweden explained this lack of cyclicity by predation by generalist predators. The result was a constant high density of predators that fed on voles in function of seasonality during others prey populations depression. It appears that predator populations were maintained by local area with high vole density and that predators switched from an area to another following vole abundance fluctuation in space. Predator numbers maintained on a landscape level by the vole fluctuations being asynchronous (Lambin et al., 1998) so that there are always some areas with high vole densities. Our results support this hypothesis of a hot spot of predators in montane water vole outbreaking area because they indicate a significative and positive statistical relation between the relative abundance of some predator species we monitored and the relative abundance of montane water vole. However, this result concern only data during decline. We expected similar results during increase phase, especially because we observed a lower lure survival during this phase, but we didn't. This observation show that predator response in our study area is maybe more complex than in the Erlinge et al. (1983) study. Following Erlinge et al. (1983) and Norrdahl and Korpimäki (2002), the numerical response of predators may be divided into three components: (i) behavioural response (immigration, emigration, predator mobility response and predator abundance), (ii) survival of existing individuals (mortality), and (iii) production of young (natality). Our results allowed us to only consider the part (i) of the potential numerical response of the montane water vole-eating predator. Indeed, we stress on the fact that for the first time we evidence that relative abundance of some vole predators (red fox, carrion crow) is positively related to the relative abundance of montane water vole in temperate context claiming for the existence of a numerical response of these predator species already known in more Nordic areas (Lindström, 1989; Small et al., 1993; O'Mahony et al., 1999).

V - Conclusion

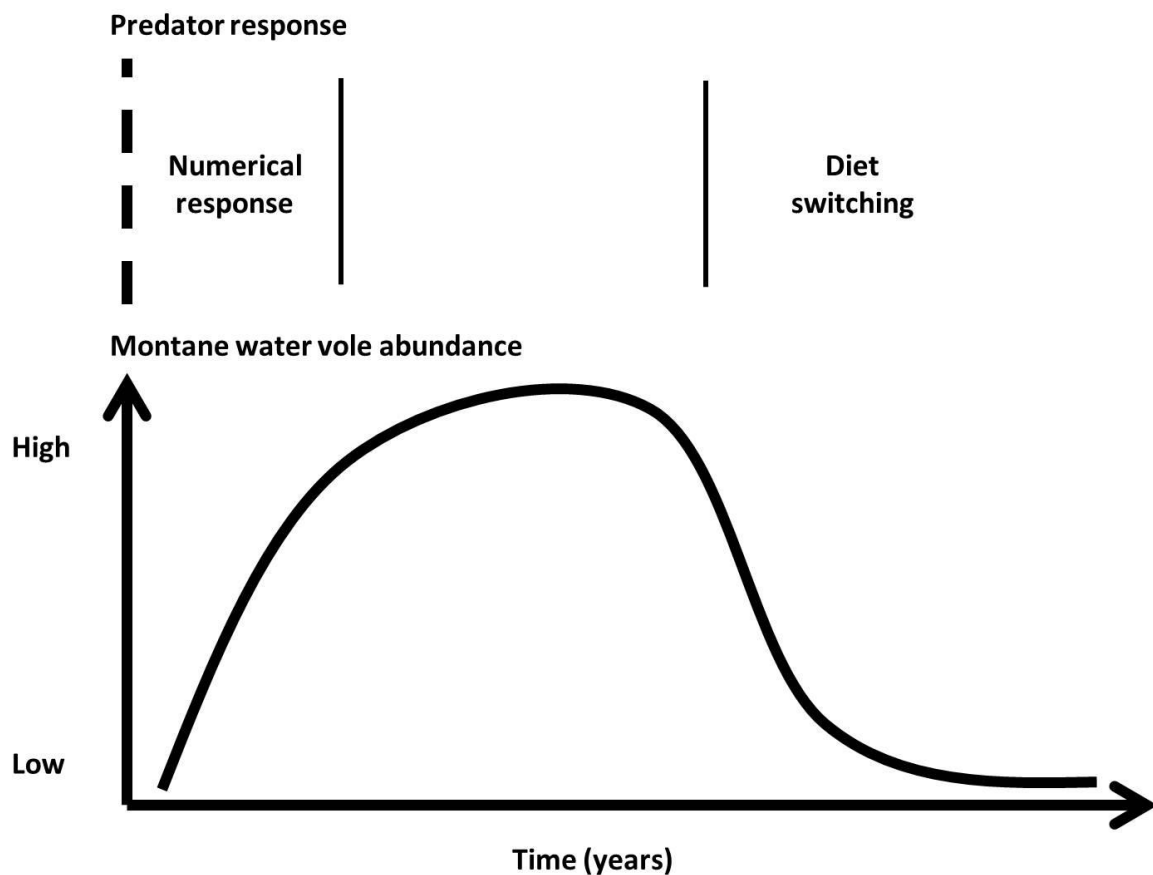


Figure 33 : Synthesis of observed responses of lure predators.

Firstly, the study allows us to consider the composition of the lure's predator feeding on a sausage lure (representing an alternate prey). This guild is composed by about 50% of mammal predators, 40% of avian predators and of 10% of undetermined predators. This experiment shows that avian predators and domestic cat found more quickly the alternative prey than other terrestrial predators. The interpretation is uneasy at this stage. It may be that bird capacity to soar permit to cover more quickly larger areas to find a prey or carrion. The positive relationship found between the abundance of montane water vole and the time before the lures remain found supports the idea of an increased predation pressure during the decline phase on alternative prey (Figure 33). Moreover, the meat lures have been found more quickly during the increase of montane water vole abundance maybe because of an increase of the predation pressure locally. Literature claimed that predation increases with the proximity to a habitat discontinuity, or an edge between two habitats creating a predation trap.

Despite the absence of effect of our landscape categories, we use the NDVI as an indirect measure of vegetation biomass. We show that the larger the vegetation biomass, the larger the lure survival. This surprising result let us hypothesized that a large vegetation biomass such as edge within grasslands provides more cover from predators. Considering our results, it appears that some avian predators (carrion crow, Eurasian magpie, red kite) found more quickly the lures than some terrestrial predators (domestic dog, red fox or badger). At least, our results show a significant statistical link between a high relative abundance of montane water vole and a longer time of undiscovery of the lures in Jura mountain. Moreover, our results show that predator densities are generally larger in areas with larger montane water vole abundance (Figure 33). However, the correlations found, although statistically significant, generally explained a small, and sometimes a nominal, amount of the total variance of the system. This clearly shows the complexity by which such relations between predators, main prey and alternate prey occur at several spatial scales.

In conclusion, it appears that the long-term monitoring of fauna and anthropic actions is essential to understand prey-predators' relationships in a context of small mammal cyclic outbreaks. Wildlife managers should take into account possible diet switchings on alternative prey population to limit the decline of focal species. Indeed, several solutions exist to manage the predator guild. The first one, hard to apply in the field but already in trial in some places of our region, consist in a diversification of landscape composition and landscape features to modify the montane water vole cycle and so the predator responses and provide places to hide for alternate preys. Another important information we brought in our study for wildlife managers is that more than 75% of lure predators are either already controllable (e.g. corvids, foxes) or domestic animal (eg. dogs, cats). The latter open the way to potential actions towards pet owners to prevent wandering (Thomas et al., 2012; Hughes and MacDonald, 2013).

Chapter III (B): Variation of predation pressure in a context of cyclic population outbreaks of grassland voles: high mountain (Alps) context.

I - Introduction

We brought new information about prey-predator relationships in the context of a montane water vole outbreak context in Chapter 2(B). However, our results were strongly limited both by methodological inaccuracies and too short-time monitoring.

However, we had the opportunity to perform a very similar experimental design as in the Jura Mountains (Chapter 3(A)) to improve our understanding of the prey predator context in the Haute-Romanche valley. Considering our knowledge (Chapter I), there is no current cyclicity in montane water vole outbreak in Haute-Romanche valley, which made it impossible to compare the results with the ones of the Jura Mountains experiment. Indeed, the only observed outbreak in the valley occurred between 1998 and 2010 (see Chapter I), according to field control program in the valley, montane water vole population seemed to be in low density phase with weak increase in some local pockets. Therefore, we were not able to take into account the phase of the outbreak as in the Jura experiment. We just looked for relationship between punctual montane water vole abundance variation and consumption of meat lures. The aim of this study is to answer one question: Are the factors driving new alternate prey consumption in the Jura similar in the Haute-Romanche valley?

II - Material and methods

II-1 Study site

The study area is set the Haute-Romanche valley (45° 02' 49" N 6° 18' 24" E), in the Alps, and was carried out from June 16th to June 28th (Figure 10)

One of the main difficulties in ecological studies when dealing with population dynamics is to place observations in a context that is inclusive enough to look at these dynamics outwardly, from the boundaries of the phenomenon under study (Lidicker, 1988). Therefore, this study was conducted on one perception level. The perception level was

defined at a smaller scale, by using more detailed and objective landscape elements (= landscape units). As for Chapter 3 (A), the 'landscape units' are 500 x 500 m cells from a grid georeferenced to the Lambert zone II system.

II-2 Alternate “prey” and experimental design

Because of the dangerousness of the Alpine study area, the field work was achieved in day time close to roads. The exposure time was 5 nights and 5 days. 35 camera traps were set on stacks at about one-meter distance from the lures (Glen et al., 2013). The location of each lure was selected among 35 meshes not selected randomly but according to their safety.

II-3 Small mammal abundance

We walked 14 times 1000 meters transects (Figure 34b) to estimate the relative abundance of small mammals (*Arvicola terrestris*, *Talpa europaea*, *Microtus* spp.) following the same method as presented in Chapter 3 (A).

II-4 Diurnal bird counts

We used the ACT (*Alaudidae*, *Corvidae*, *Turdidae*) method to count *Alaudidae*, *Turdidae*, *Phasianidae*, *Colombidae* birds as potential alternative preys and *Corvidae* birds as potential predators (Roux et al., 2012). On 5-kilometer transects (2 in the Alps mountains (Figure 34c)) on every 1-kilometer point, the observer records the number of each species by listening and watching in a circle of 500-meter radius.

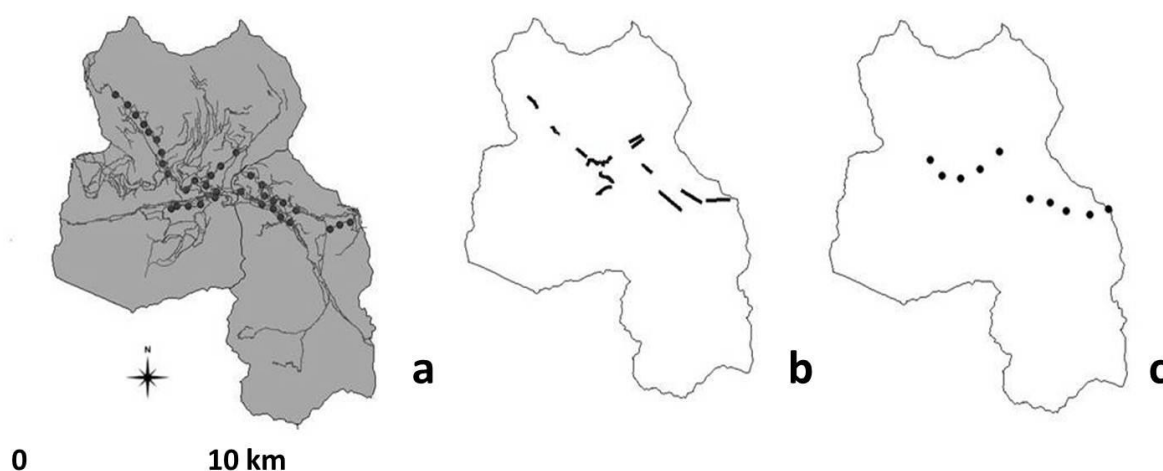


Figure 34 : Organization of wildlife survey: meat lure and night counting (a), small mammals (b) and diurnal bird survey (ACT and bird of prey (c)).

II-5 Spatial interpolation of montane water vole relative abundance

Montane water vole and camera trap results not being collected on the same sampling grid, interpolation on a common grid was necessary. We chose to use a General Additive Model (GAM) to compute a trend surface of montane water vole relative abundance as detailed in Chapter III-A.

Correlations between our response variable (time before lures discovery) and our independent variable (montane water vole abundance) were computed at a 500-meter radius buffer centred on each camera trap resolution over the whole study area. Therefore, each experimental camera trap device was associated with an interpolated montane water vole index.

II-6 Statistical analysis

(1) In order to test whether there is a statistical difference between the variations of the lures discovery time according to the type of predators we computed an Age-Specific Hazard Models.

(2) In order to test if there is a statistical difference between the lures discovery time according to the GAM-modeled relative abundance of montane water vole we used General Linear models (GLM) following a Poisson distribution as presented in Chapter II-B.

II-7 Computing environment

Spatial analysis and GIS data management were performed using Quantum GIS 1.8.0-Lisboa (Quantum Gis, 2013), GRASS GIS 6.4.2 (Grass Development Team, 2012) and R 2.15.1 (R-Core Team, 2012b) using the packages car (Fow and Weisburg, 2011), foreign (R-Core Team, 2012a), maptools (Lewin-Koh et al., 2012), mgcv (Wood, 2011), pgirmess (Giraudoux, 2012), raster (Hijmans and Van Etten, 2012), rgdal (Keitt

et al., 2012), rgeos (Bivand and Rundel, 2012), Rlab (Boos and Nychka, 2012), sp (Bivand et al., 2008).

III - Results

III-1 Predator guild composition

In the Alps, 49% of the lures were discovered. Red fox, dogs, northern raven and Eurasian magpies were the main predators with respectively 30% (n=5), 18% (n=3), 18% (n=3), 23% (n=4) of presence each. Eurasian magpies represented 10% of observed predators. Other predators were more sporadically observed such as European badgers (n=1) and domestic cats (n=1).

III-2 Response of predators to the presence of the lures

Figure 35 shows that the mean value of discovery time of the lures was larger for the red fox (mean time = 85 +/- 0.36 hours) than for the domestic cat (mean time = 34 +/- 0.47 hours), the northern raven (mean time = 51 +/- 0.37 hours), the Eurasian magpie (mean time = 7 +/- 0.38 hours) and the domestic dog (mean time = 39 +/- 0.39 hours) (Age-Specific Hazard Model, 0,0001 < P-value < 0,02) (Figure 35). This phenomenon is the same for the European badger (mean time = 60 +/- 0.33 hours) which present a mean value of time of discovery of the lures later than for Eurasian magpie (Figure 35).

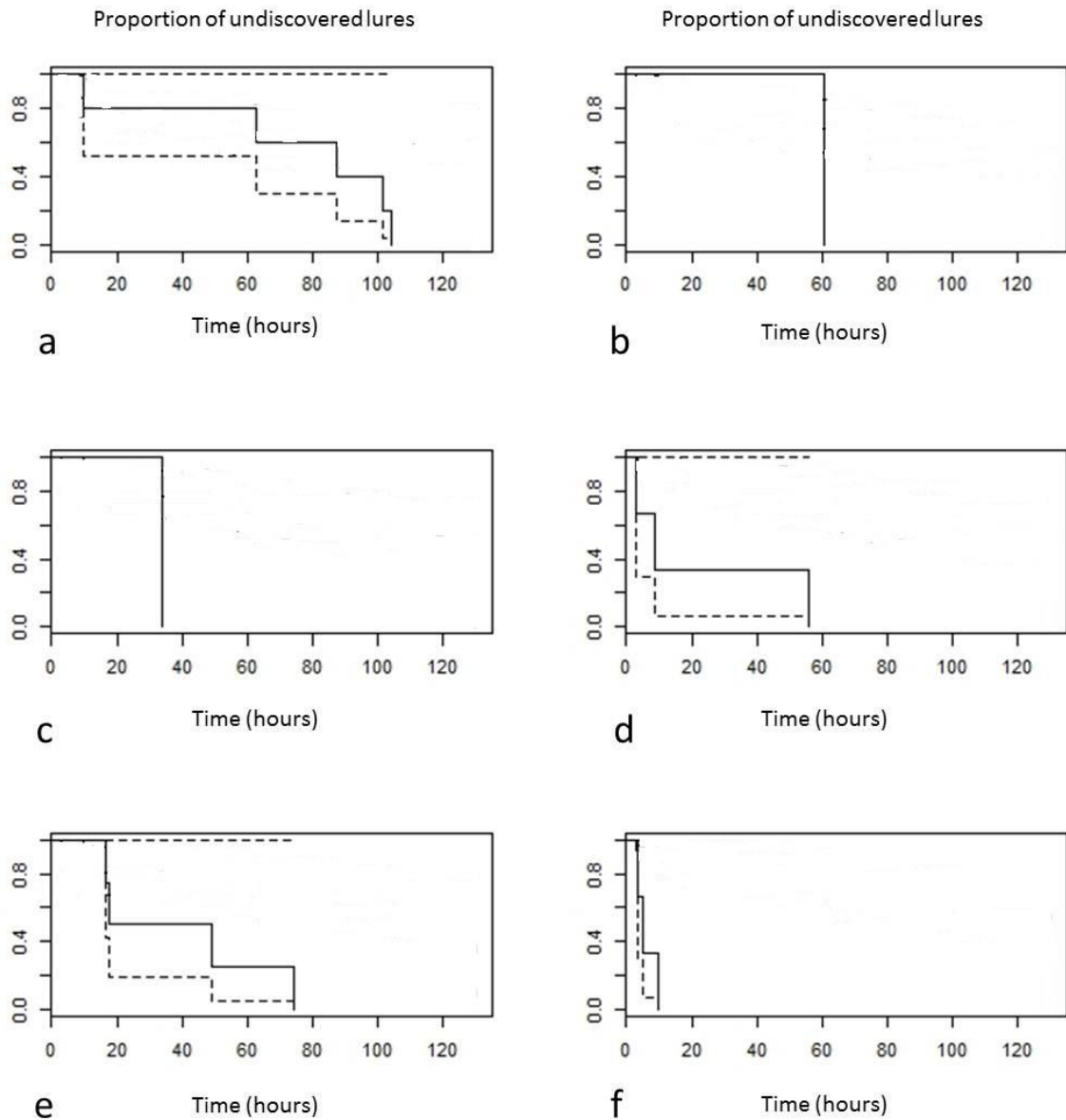


Figure 35 : Proportion of undiscovered lures during time (hours) regard on predators: a (red fox (n=5)), b (badger (n=1)), c (domestic cat (n=1)), d (domestic dog (n=3)), e (northern raven (n=4)), f (Eurasian magpie (n=3)).

III-3 Montane water vole abundance and lure discovery

Studying the relationship between the montane water vole relative abundance and the time before the discovery of the lures, we observed that it exists a positive correlation between our two variables which means that when montane water vole relative abundance increases, time for lure discovery increases too (ANOVA, p -value < 0.0001; $R^2 = 0.03$). As explained before, the only observed outbreak in the valley occurred before our experiment (see Chapter I), looking for field control program observations, montane water vole population seemed to be in low density phase (median value of montane water vole transects = 4.5% of positive intervals) with a weak increase in some local pockets (maximum relative abundance reached 46% of positive intervals). Therefore, we were not able to take into account the phase of the outbreak as in the Jura experiment.

IV - Discussion

IV-1 Comparison between Jura and Alps context

Only considering comparison of results on the relationships between montane water vole relative abundance and lure survival, it appears that the ones obtained in the both mountains context are very similar. Unfortunately, we were not able to compare results with the ones of the Jura regarding the history of the cycle. This strongly limited the comparison between the two systems and revealed the need for a continuous monitoring of small mammals to observe changes of vole abundance over several years. About the predator guild composition, the only great difference is the replacement of the carrion crow in the middle mountain of the Jura by the northern raven in the alpine context. Marquiss et al. (1978) found that abundance of northern ravens in Scotland was correlated with elevation, with more pairs of breeding in high altitude. In the Haute-Romanche, it appears that avian predators (Eurasian magpie, northern raven) found the lures more quickly than other terrestrial predators (domestic dog, red fox or badger), corroborating the results found in the Jura Mountains (carrion crow, red kite, Eurasian magpie, common buzzard). Here our results, similarly to those found in the Jura Mountains, show a significant positive correlation between a high relative abundance of montane water vole and a better lure survival. This similarity suggests that montane water vole abundance may impact predation on an alternative food resource similarly. Unfortunately, we cannot corroborate this finding with the

literature because our study is the first one in an alpine context of population density variations of montane water vole population.

V - Conclusion

Results obtained in two different mountain contexts appear to be very similar. In both mountains most avian predators found the lures more quickly than most terrestrial predators. In both cases, larger population densities of montane water vole increase the time for lure discovery. This suggests a potential diet switching in both areas. However, there were several limitations to compare both areas. Firstly we were not able to characterize the phase of the outbreak for each camera trap limiting our analysis to the single correlation between punctual relative abundance and lure survival. Secondly, we were not able to collect reliable data on predator abundance and therefore compare the predator abundance response with the Jura Mountains context.

Discussion générale

I - La spécialisation herbagère, un facteur commun aux massifs montagneux français dans le développement de pullulations de campagnol terrestre. Une comparaison entre Massif Jurassien, Massif Central et vallée alpine.

En se basant sur les connaissances déjà existantes sur les pullulations des micro-mammifères en général et sur celles du campagnol terrestre en particulier, nous avons pour objectif d'étudier l'impact potentiel de la spécialisation agricole vers la production herbagère sur le développement de pullulations de campagnol terrestre dans une zone de haute-montagne nouvellement touchée.

Dans un premier temps nous avons constaté le scénario historique agricole similaire entre cette vallée de la Haute-Romanche et d'autres zones montagnardes européennes, à la différence près que dans la vallée de la Haute-Romanche, l'emplacement des zones fauchées et des zones pâturées sont fortement dépendantes de l'altitude considérée. Entre le début du 19^{ième} et le début du 21^{ième} siècle, la production agricole s'est spécialisée sur la production herbagère avec comme effet direct la disparition virtuelle des zones labourées, le cantonnement des zones de fauches dans les fonds de vallée et l'extension des zones de pâtures au reste des zones exploitées pour l'agriculture (Girel et al., 2010).

En se basant sur l'occupation du sol et l'abondance relative en campagnol terrestre, nous avons pu mettre en évidence un lien de cause à effet à l'échelle parcellaire entre l'occupation du sol actuelle et l'intensité de la pullulation du campagnol terrestre. S'il s'avère que tous les types d'occupation agricole ont été touchés par la présence de campagnol terrestre, comme dans le cas des Massifs du Jura et du Massif Central (Morilhat et al., 2007, 2008), les zones pâturées ont présenté une amplitude de l'abondance en campagnol terrestre moins importante que les zones fauchées notamment. Bien qu'un résultat similaire soit attendu pour les zones labourées (connues pour être défavorables au campagnol terrestre dans le Jura (Morilhat et al., 2007, 2008)), il s'avère que la surface labourée est devenue bien trop peu importante pour constituer un obstacle à la pullulation du campagnol terrestre dans le cas précis de la Haute-Romanche. Si cette étude a permis de mettre en avant l'effet de l'occupation du sol actuelle sur l'amplitude des pullulations de campagnol terrestre en

haute montagne, aucun effet de l'histoire agricole des parcelles n'a pu être démontré. Néanmoins, l'occupation agricole actuelle étant directement dépendant de l'histoire agricole de la vallée, il apparaît clairement que la spécialisation agricole vers la production herbagère dans cette vallée est à l'origine du développement de cet épisode de pullulation du campagnol terrestre.

Sur le plan du fonctionnement spatio-temporel de cet épisode de pullulation du campagnol terrestre, hormis la cyclicité du phénomène qui reste à observer compte tenu de l'aspect relativement nouveau du phénomène dans cette vallée, il existe de grandes similitudes avec les connaissances déjà acquises dans le Massif du Jura et en Auvergne. Ainsi, le développement temporel de la variation de l'abondance relative en campagnol terrestre à l'échelle parcellaire montre un processus étalé sur environ 5 années avec au moins une période de pic puis une période de déclin suivie d'une période de faible abondance. L'absence d'observation d'une phase de croissance lente peut être due à la méthode de suivi employée sur de larges échelles spatiales ne permettant pas nécessairement de détecter les premiers indices d'occupation des parcelles. D'un point de vue spatial, l'épisode de pullulation a montré une diffusion spatiale sous la forme d'une pseudo vague voyageuse (ou vague de colonisation ?) canalisée par le relief, partant du Nord-Ouest depuis le lieu-dit La Buffe, vers le Sud-Est en suivant le vallon du Gâ, puis remontant la vallée de la Romanche jusqu'au Col du Lautaret vers l'Est. De manière analogue aux vagues voyageuses Jurassiennes (Berthier et al., 2013), la propagation spatiale de cet épisode de pullulation de campagnol terrestre a été fortement canalisée par les discontinuités paysagères marquées dans cette zone de haute montagne. En effet, en plus d'avoir scrupuleusement suivi les fonds de vallées (vallées de la Buffe, de la Haute-Romanche, du vallon de Valfroide) cette propagation spatiale a été freinée à trois reprises, soit par de très fortes pentes, soit par la présence de zones habitées par l'homme et, dans le dernier cas, d'une gorge parcourue par un torrent de montagne. Il est à noter que la vitesse de propagation dans cette vallée alpine est fortement inférieure à celle enregistrée dans le Jura (respectivement un maximum d'environ 4 km/an contre 12 km/an). Cette faible vitesse pourrait être mise sur le compte des discontinuités paysagères plus marquées dans cette vallée alpine que sur les plateaux Jurassiens, ce qui reste à tester.

Concernant le phénomène de pullulation dans cette vallée, plusieurs questions restent en suspens et pourraient fournir des pistes de recherche intéressantes. Tout d'abord le fait de savoir si ce phénomène de pullulation va, comme dans le Jura et dans le Massif Central, devenir un phénomène cyclique. A l'heure actuelle, un programme de piégeage annuel renouvelé chaque année depuis 2010 permet un suivi relativement fin de l'état des populations de campagnol toujours actives dans la vallée. La deuxième question est de savoir d'où viennent ces campagnols terrestres sachant que cette vallée était considérée comme « vierge de campagnol terrestre » avant 1998. Cette question est d'autant plus intéressante qu'il y a sans doute eu deux foyers d'émergence non connectés de la pullulation et que, durant la phase de terrain de ce travail, des taches de campagnol terrestre ont été observées dans des zones que le protocole d'observation et de piégeage ne permettent pas de détecter. En effet, ces protocoles ne couvrent pas certaines zones très isolées à proximité d'une vallée voisine (Besse) déjà connue pour être touchée depuis plusieurs années par des pullulations. Cette question peut trouver réponses par l'utilisation des différents outils de génétique des populations et de phylogéographie pour essayer de comprendre les flux populationnels potentiels entre chaque vallée alpine. Par exemple Pierny et al. (2005) ont comparé, au Royaume-Uni, l'ADN mitochondrial de différents campagnols terrestres dans le but d'obtenir des informations quant à leur proximité génétique par rapport à différentes populations du continent européen.

II - Étude du report de prédation, utilisation des suivis à long terme de la faune sauvage et du régime alimentaire, deux approches nécessaires mais pas suffisantes.

Une des questions principales de ce travail de thèse était d'étudier l'effet potentiel du développement de pullulations de campagnol terrestre dans nos deux zones d'études (Massif Jurassien et vallée alpine de la Haute-Romanche) sur les prédateurs. Selon la zone d'étude, deux méthodes différentes ont été mises en œuvre, pour des raisons logistiques et pour répondre (en la canalisant sur des compromis raisonnables) aux demandes des organismes cynégétiques et du Parc des Ecrins. Dans le Massif Jurassien, l'utilisation de suivis à long terme effectués par la Fédération Départementale des Chasseurs du Doubs a permis de confronter l'évolution spatio-temporelle de l'abondance relative du renard roux, du lièvre d'Europe et du campagnol terrestre. En Haute-Romanche, l'absence de suivis à long terme nous a conduits à

nous orienter vers l'analyse du régime alimentaire du renard roux par la méthode d'analyse des macro-restes, induisant ainsi, deux types de questionnement différents.

II-1 Massif Jurassien

Avant d'avoir pu confronter l'abondance relative des trois espèces suivies dans le département du Doubs nous avons dû analyser la variation de l'abondance du lièvre d'Europe et du renard roux dans le temps. Il est apparu, qu'en accord avec la bibliographie actuelle (Edwards et al., 2000; Schweiger et al., 2007), les deux espèces présentaient des tendances temporelles respectivement à la diminution et à l'accroissement. Après détendage des données des deux espèces suivies et en accord avec les résultats obtenus par Jacquot et al. (2013) sur le même jeu de données, nous avons également tenu compte du fait que l'utilisation de rodenticides sur notre zone d'étude modifiait l'abondance relative du renard roux dans l'espace et dans le temps. L'abondance relative du renard roux, détendue aussi pour l'usage de la bromadiolone, présente une évolution temporelle parabolique. L'interprétation de cette tendance surprenante est loin d'être claire. Une dernière variable, non prise en compte dans l'analyse concerne une éventuelle épidémie de gale sarcoptique. Néanmoins durant la durée de l'étude aucune donnée n'était disponible. Depuis 2013, la Fédération Départementale des Chasseurs du Doubs collecte des données sur cette hypothèse ce qui pourra peut-être permettre de la tester dans un futur proche.

Après avoir pris en compte ces facteurs dans notre analyse, il apparaît qu'il existe une relation statistique négative entre l'abondance relative du lièvre d'Europe et celle du renard roux. Dans le même temps il existe également une relation positive entre l'abondance relative en lièvre d'Europe et celle du campagnol terrestre. Cette dernière peut être considérée comme une indication d'un potentiel report de prédation du renard roux sur le lièvre d'Europe. Néanmoins cette conclusion présente comme limite majeur le fait de ne jamais inclure d'analyse de régime alimentaire (ni qualitatif ni quantitatif, ni par analyse des macro-restes ni par une approche moléculaire) du renard roux durant la même période nécessaire pour renforcer l'hypothèse du report de prédation (Dupuy et al., 2009). De plus, elle n'explique qu'une part infime de la variance observée. Cette dernière observation confirme les conclusions d'études précédentes qui place la prédation comme un facteur aggravant du déclin du lièvre d'Europe mais qui insiste sur l'importance d'autres facteurs majeurs comme

l'intensification agricole, les conditions climatiques ou encore les maladies (Péroux, 1995; Edwards et al., 2000; Vaissaire et al., 2005; Cardarelli et al., 2010; Decors et al., 2011).

II-2 Haute-Romanche

En travaillant sur la récolte de fèces de renard roux en Haute-Romanche, nous avons observé que sur des parcours fixes nous récoltions 4 à 5 fois plus de fèces en automne qu'en été et que durant l'automne les fèces étaient situées plus près des zones habitées. De nombreuses limites quant à la détection des fèces de renard sont avancées dans la littérature (Cavallini, 1994) telles que de fortes pluies, une végétation plus ou moins importante, des chutes de neige, etc. Ici nous ne pouvons pas conclure sur la variation saisonnière que nous observons sur la collecte de fèces faute d'un protocole adapté qui aurait permis de prendre en compte les facteurs évoqués ci-dessus. Concernant la diminution de la distance aux villages des fèces récoltées durant l'automne, l'hypothèse proposée est la diminution ou la disparition de ressources alimentaires estivales (marmottes, bétail, insectes) et la dégradation des conditions climatiques en altitude (premières chutes de neiges) forçant les renards roux à redescendre dans la vallée. Néanmoins, à nouveau, nous en resterons au stade de l'hypothèse en raison de l'absence d'un protocole adapté pour vérifier notre hypothèse. Une première suite à donner à cette étude serait d'utiliser l'ADN extrait durant la thèse pour vérifier si une approche moléculaire (séquençage massif) permettrait d'augmenter la détection des items alimentaires utilisés par le renard roux. Elle permettrait également de constater si l'on peut obtenir un nom d'espèce pour chacune des ressources. Idéalement, cette nouvelle approche moléculaire devra être appliquée sur un minimum de 10 années avec une récolte mensuelle permettant d'obtenir à la fois la variation du régime alimentaire en fonction de la saison et d'englober l'arrivée d'un nouvel épisode de pullulation dans la vallée. En parallèle, une mesure de la variation d'abondance mensuelle d'un nombre maximal de ressources (campagnol prairiaux, oiseaux, méso-mammifères, carcasses d'ongulés, fruits, insectes) permettrait de distinguer la consommation d'une ressource en lien avec la saisonnalité et en lien avec un report de prédation potentiel.

Notre étude a permis d'apporter des informations sur la composition du régime alimentaire du renard roux en Haute-Romanche en été et en automne 2014. Nous

avons observé une forte occurrence d'insectes (et notamment d'orthoptères) dans le régime alimentaire du renard. Le campagnol terrestre et les campagnols du genre *Microtus* représente les micro-mammifères à l'occurrence la plus élevée dans les fèces de renard roux.

Ces résultats mettent en évidence les limites actuelles dans la compréhension de la réponse fonctionnelle d'un prédateur avec de multiples options de proies, à savoir l'effet de plusieurs ressources alimentaires et de leurs possibles interactions sur la variation du régime alimentaire du renard roux. Pour aller plus loin dans l'étude de ce système, il faudrait déterminer la portée du domaine vital du renard roux dans notre zone d'étude et de le comparer avec notre échelle d'interpolation. Une dernière possibilité serait d'élargir l'échelle spatiale étudiée pour englober au mieux toutes les possibilités de taille de domaine vital d'un renard roux.

Enfin, l'utilisation de la méthode d'analyse du régime alimentaire par macro-restes a montré des limites quant à l'apport d'information à notre système. Dans la méthode utilisée pour l'étude du régime alimentaire, l'utilisation de caractères biométriques pour l'identification d'une espèce à partir de macro-restes fragmentaires présente une difficulté dans l'identification précise des items alimentaires :

- du fait de la mauvaise qualité physique souvent observée des macro-restes, l'observateur peut se tromper quant à la détermination qu'il obtient (Valentini et al., 2009).

- le degré de digestibilité variant en fonction de la ressource alimentaire considérée, certains groupes taxonomiques vont être, au mieux, sous-estimés dans le régime alimentaire au pire être absent alors qu'ils ont été consommés.

Ainsi, il a été impossible de statuer sur la nature des proies de tailles importantes (tétraoonidés, lagomorphes, marmottes, etc.) particulièrement intéressantes pour les partenaires de la thèse.

Par conséquent, l'analyse du régime alimentaire dans la vallée de la Haute Romanche devra se saisir des avancées en matière de séquençage génétique de masse et de

bio-informatique. Malgré des biais inhérents à la méthode (qualité de l'ADN en fonction de la nature de l'aliment, coût financier, nécessité d'un référentiel spécifique de séquences ADN) (Valentini et al., 2009), cela permettra de préciser le spectre qualitatif du régime alimentaire du renard, voire même de se focaliser sur un ou plusieurs taxons en particulier. L'ADN ayant été extrait lors de cette étude, mais pas analysé dans sa totalité, il est possible de donner rapidement une suite à ce travail.

III - Apport d'une approche expérimentale de terrain dans la prise en compte des relations proies-prédateurs dans un contexte de pullulations de campagnol terrestre.

Après l'utilisation dans le Chapitre II de deux approches méthodologiques différentes dans deux zones d'étude différentes, le faisceau d'indice plaidant en faveur d'un report de prédation dans nos systèmes reste trop fragmentaire.

Toujours sur ces deux zones d'études, nous avons développé une approche expérimentale de la prédation par ajout et surveillance photographique d'une nouvelle « proie ». Les biais potentiels de cette expérimentation ont été pris en compte (présence du piège photographique dans l'environnement, détectabilité du leurre carné, etc.) (Glen et al., 2013).

La première information que nous apportent cette expérimentation est la composition de la guildes des prédateurs et leur vitesse à consommer le leurre. Cette guildes est composée à 50% par des mammifères dominés par le renard roux et les animaux domestiques (chat et chien), à 40% par l'avifaune prédatrice dominée par les corvidés et dans 10% des cas par des prédateurs non identifiés. Cette expérience nous a permis de constater une différence de vitesse de découverte du leurre carné en fonction du type de prédateur considéré. Ainsi l'avifaune prédatrice découvre plus rapidement les leurres carnés que la plupart des prédateurs terrestres (le chat domestique présentant la même réponse que l'avifaune) notamment en raison de leur moyen de locomotion leur permettant de couvrir plus rapidement de plus grandes surfaces (DeVault et al., 2003).

La catégorisation par lecture de cartes IGN et d'orthophotographies en deux grandes typologies du paysage n'as pas permis de détecter d'effets de nos catégories sur la

consommation du leurre. En utilisant une approche par analyses de données satellites infrarouges, nous avons détecté un effet positif de l'augmentation de biomasse végétale en milieu agricole sur la survie du leurre carné plaidant pour l'hypothèse d'un effet protecteur des éléments végétaux fixes du paysage (haies, prés-bois, etc.). Néanmoins, au vu de la faible part de variance expliquée par notre approche, nous nous devons de rester prudents quant à cette observation. Pour renforcer nos conclusions, il conviendra de faire appel aux compétences de géomaticiens et de géographes pour obtenir des données d'occupations du sol à l'échelle de la zone d'étude et de résolution très fine pour prendre en compte les éléments fixes du paysage (haies, bosquet, arbre isolé, etc.) (inférieurs à 5 mètres) pour investiguer de manière particulière l'effet réel supposé de la structure paysagère (Foltête et Giraudoux, 2012).

Durant la phase d'augmentation de l'abondance en campagnol terrestre, la survie des leurres carnés a été moins bonne que lors des phases de déclin et de basse abondance. Dans un cas particulier suédois (Erlinge et al., 1983), il a été démontré que les prédateurs généralistes avaient tendance à se déplacer d'une zone de pullulation à l'autre pour trouver une source de nourriture stable et abondante auprès des populations de micro-mammifères. La relation statistique positive entre l'abondance de certains prédateurs (renard roux, corneille noire, milan royal) et l'abondance en campagnol terrestre que nous observons conforte cette hypothèse. Sachant que la réponse numérique des prédateurs peut être décomposée en trois composantes : 1) le comportement (immigration, émigration, mobilité spatiale), 2) la mortalité des prédateurs et 3) la natalité, nos résultats nous permettent d'envisager une réponse numérique partielle des prédateurs cités ci-dessus via une mobilité spatiale des individus d'une zone de pullulation de campagnol terrestre à une autre. Ce résultat s'affirme comme une information nouvelle dans des systèmes tempérés tels que nos zones de moyennes montagnes.

Nous avons montré une relation positive entre la survie du leurre carné et l'abondance relative en campagnol terrestre. Ce résultat représente à nouveau une indication potentielle de l'existence d'un report de prédation dans notre expérimentation. La reconduction de cette expérimentation dans la vallée alpine de la Haute-Romanche nous a apporté des observations similaires. Ceci nous a permis de renforcer nos

conclusions concernant la survie du leurre carné en fonction de l'espèce prédatrice observée ainsi que le faisceau d'indices plaidant en faveur d'un report de prédation et donc d'une réponse fonctionnelle des prédateurs. Néanmoins, il conviendrait de préciser ces résultats en considérant également l'historique de la pullulation pour confirmer que cette réponse fonctionnelle a bien lieu uniquement durant la phase de déclin. Cependant, la faible part de variance expliquée dans chacune de nos analyses dans les deux zones d'études affaiblit la puissance de ce faisceau, et relativise l'importance de la prédation vis-à-vis d'autres facteurs inconnus, et ne nous permet donc pas de conclure de façon forte sur la réponse numérique des prédateurs dans nos contextes.

Conclusion générale de la thèse

En matière d'apport scientifique, le résultat cœur de la thèse est la présence dans nos deux zones d'études d'un faisceau de résultats en faveur de l'existence d'un phénomène de report de prédation de la guilda de prédateur des campagnols prairiaux sur la petite faune de montagne d'intérêt cynégétique et/ou patrimoniale. Néanmoins, afin de consolider ce faisceau de résultats il conviendra de continuer les actions de monitoring à long terme déjà engagées, notamment dans le Doubs, et de les développer dans les zones alpines. La mutualisation des différentes techniques mises en place dans ce travail doctoral (monitoring de l'abondance des campagnols prairiaux, des prédateurs et des proies, suivi de l'évolution de l'occupation du sol, analyse du régime alimentaire de certains prédateurs) doit être confortée, élargie, mise à niveau d'un point de vue technique (utilisation des outils génétiques, bio-informatique) et perdurée sur une longue période pour confirmer ou infirmer les conclusions de ce travail de thèse. Le simple fait de vouloir travailler sur les aspects de variation temporelle des processus écologiques impactés par les pullulations cycliques de campagnols prairiaux nécessiterait un suivi d'au moins dix ans pour englober dans sa totalité un épisode de pullulation. Pour prendre en compte des phénomènes existants sur le très long terme la mise en place de toutes les techniques citées ci-dessus sur plus de trente années serait idéalement à envisager (changement climatique par exemple ou modification de la structure des cycles sur plusieurs décennies (Butet et Spitz, 2001)).

D'un point de vue des perspectives de recherche, toujours en lien avec une ré-orientation technique des résultats auprès des différents partenaires, voici mes différentes propositions résumées dans la Figure 36 :

- Mettre en place un programme de recherche complet sur une approche d'écologie historique. Ce travail viserait à rechercher et à compiler toutes les informations anciennes disponibles sur les pullulations de campagnols prairiaux et leur environnement (e.g. écrits historiques, données de piégeage anciennes, ouvrages anciens sur l'occupation du sol). L'objectif à court terme serait d'évaluer le niveau de finesse de ces informations sans doute fragmentaires puis de tenter de reconstruire une série temporelle des deux siècles passés pour les campagnols prairiaux. Si cet objectif est atteint

il permettrait d'approfondir les connaissances par exemple sur l'impact des changements agricoles anciens sur le fonctionnement spatio-temporel des populations de campagnol prairiaux. Il permettrait également de s'intéresser à l'impact potentiel du changement climatique sur le système campagnol prairial, travail qui pour l'instant n'a jamais été réalisé sur nos zones d'études.

- En parallèle à cette approche historique du système étudié, le renforcement et le développement des systèmes d'observations à long terme du système (abondance des proies et des prédateurs, régime alimentaire amélioré par l'approche moléculaire, suivi du paysage, suivi du climat) permettra si les résultats le permettent de poursuivre la construction de la série temporelle pluri-séculaire obtenu par l'approche historique. D'un point de vue technique, cela permettra potentiellement de mesurer l'effet de l'application des outils de gestion obtenus via la recherche entreprise sur le campagnol depuis plus de trente ans (re-diversification paysagère, monitoring de la faune sauvage, régulation des prédateurs, réglementation de la lutte chimique contre le campagnol, etc.). D'un point de vue social, cette approche pourrait permettre de poursuivre les efforts entreprise depuis de nombreuses années pour fédérer tous les acteurs autour de la question de la gestion du problème campagnol (organisations agricoles, cynégétiques, environnementalistes, politiques et scientifiques) via la collecte des données et le suivis des différents programmes d'actions et de leurs résultats.
- Ces deux grandes perspectives apparaissent fondamentales pour appréhender la gestion d'une problématique nouvelle et pour l'instant peu prise en compte dans l'évolution du système, à savoir le changement climatique.

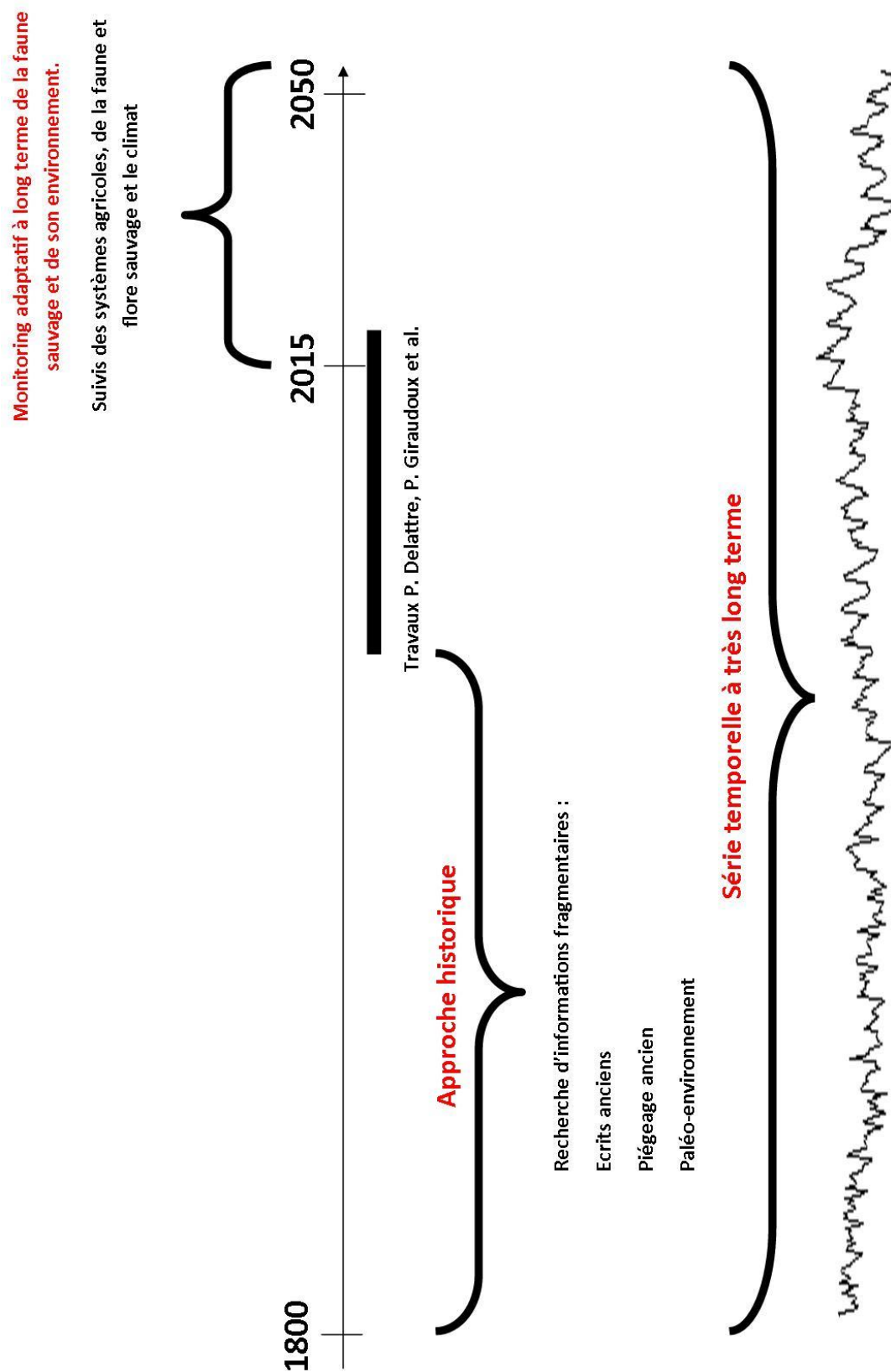


Figure 36 : Conclusions et perspectives de recherches consécutives à ce travail doctoral.

En matière d'apport technique, ce constat amène donc à une réflexion à engager sur les moyens à mettre en œuvre pour limiter ce report de prédation potentiel sur des espèces dont le statut de conservation est déjà fragilisé à l'échelle locale, nationale voir européenne et sur le rapport coût/bénéfice d'un paramètre, qui dans cette étude, n'apparaît pas comme primordial vis-à-vis d'autres facteurs. Un des résultats est la présence possible d'un effet positif qualifiable « d'effet refuge » de la biomasse végétale sur la survie des leurres carnés. La conclusion de cette thèse renforce, à mon avis, l'idée qu'il faut attaquer la problématique globale du campagnol terrestre à la source c'est-à-dire travailler sur une rediversification paysagère. Il est évident qu'un retour à une agriculture séculaire n'est pas techniquement et économiquement envisageable pour la profession comme pour toutes les activités dépendantes de l'agriculture de montagne. En revanche, des avancées réalisées sur la réimplantation de céréales et la sauvegarde des zones non exploitées (murgers, haies, lisières forestières, buissons) doivent devenir le modèle à suivre pour tenter de limiter le phénomène de pullulations du campagnol terrestre via la gestion raisonnée du paysage agricole. Concernant la gestion de la prédation, les outils de régulation des prédateurs doivent être utilisés après concertation avec les différents organismes institutionnels en raison des questions économiques, éthiques et sanitaires que cette régulation éventuelle soulève. Ainsi, le message de la régulation d'une espèce consommatrice de campagnol terrestre auprès du monde agricole doit faire l'objet d'une approche très pédagogique pour justifier d'un choix pouvant être mal compris par la profession. Concernant le volet éthique, l'existence d'un sentiment de défiance envers certaines techniques de régulation des nuisibles doit également faire l'objet d'une approche pédagogique auprès du monde environnementaliste et écologiste. Ces informations sont très importantes car elles démontrent que les prédateurs principaux des leurres carnés sont soit des espèces domestiques (chien, chat), dont la divagation est réglementairement interdite, soit des espèces sauvages qui font déjà l'objet de mesures réglementaires et/ou techniques (ex. statut de nuisibles pour des espèces telles que le renard roux et la corneille noire). Pour renforcer les actions de terrain, la première des actions est la conservation et/ou le renforcement des systèmes d'observations de la faune sauvage sur le long terme et sur de larges échelles spatiales pour apporter des informations complémentaires sur les espèces et mesurer les effets potentiels des actions de gestion entreprises.

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