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Évolution culturelle du chant d'oiseau en laboratoire

Sous la direction de **Sébastien Derégnaucourt et Nicole Geberzahn**

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Cultural evolution of birdsong in the laboratory

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Cultural evolution of birdsong in the laboratory



[1]

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FOREWORD

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" Les connaissances se développent aussi bien grâce aux rares découvertes de grande importance que par l'accumulation de petits résultats. "

Vladimir Kourganoff

" De l'observation naît la connaissance. De la connaissance naît le respect. "

Nicolas Davy

NOTES TO READERS

This PhD project is constituted of several scientific papers written independently, each paper representing a chapter of the thesis. Therefore, the reader might find some redundancies from one chapter to another. References of the general introduction and general discussion were merged and placed at the end of this manuscript.

Paper 1

"Towards artificial song dialects in the zebra finch"

Lucille Le Maguer, Nicole Geberzahn, Laurent Nagle & Sébastien Derégnaucourt

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Paper 2

"Female preference for artificial song dialects in the zebra finch (*Taeniopygia guttata*)"

Lucille Le Maguer, Sébastien Derégnaucourt & Nicole Geberzahn

In preparation

Paper 3

"Do song dialects influence social learning in the zebra finch (*Taeniopygia guttata*)?"

Lucille Le Maguer, Alice Araguas, Bahia Guellai, Nicole Geberzahn & Sébastien Derégnaucourt

In preparation

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General Introduction

I) THE PRINCIPLE OF CULTURE

1) What is culture and how to define it?

Culture is one of the main aspects defining human civilisations, but for years now, the topic of culture in nonhuman animals has received unprecedented attention (Heyes & Galef, 1996; de Waal, 2001). There is accumulating evidence that many animal species do have culture as well. However, defining culture has been difficult (for some definitions of culture, see Rendell & Whithead, 2001) and there was and still is a huge disagreement between researchers in the use of the term "culture" applied to nonhuman animals (Galef, 1992). One definition in which the "culture" label can benefit any species is the one that considers culture as "all group-typical behavioural patterns, shared by members of animal communities that are, to some degree, reliant on socially learned and transmitted information" (Laland & Hoppitt, 2003; Laland & Janik, 2006). This definition is broad and should allow scientists to better understand the evolutionary roots of culture, to better detect relationships between culture-like phenomena in diverse taxa and it should encourage an exchange of findings and methods between the social and biological sciences, rather than emphasizing the uniqueness of human culture (Laland & Hoppitt, 2003). For these reasons, we will adopt this definition of culture as our working definition throughout the thesis.

There are two key characteristics of culture: 1) the fact that culture arises necessarily from socially transmitted information and not from individually acquired knowledge or skills, neither from information that would have been inherited genetically; and 2) culture leads to within-group similarity but also between-group differences (Durham, 1991; de Waal, 2001). Following these prerequisites of culture, Laland and collaborators (2009) define cultural variation as inter-individual phenotypic differences, which are observed within or between populations, and attributable to differences in what individuals learned socially.

2) Social learning, a prerequisite for culture

Social learning is the ability to learn from others (Boyd & Richerson, 1988), or more precisely, a "process through which one individual (the demonstrator) influences the behaviour of another individual (the observer) in a manner that increases the probability that the observer learns" (Laland, 2008). The mechanisms of social influence or social learning that are necessary for cultures to arise are diverse such as 1) social facilitation: when the simple presence of conspecifics has an effect of the individual's motivation to learn (Clayton, 1978; Zajonc, 1965); 2) stimulus or local enhancement: when a behaviour is learned by the individual itself, following the observation of a conspecific that would have socially attracted the observer's attention towards an object or a location (Thorpe, 1956); 3) imitation, a process of copying the novel action of a conspecific after a close observation: learning the sequence or combination of the conspecific's action (Whiten, 2000); or 4) emulation: when the individual learns the outcome of the conspecific's action but not its motor pattern (Whiten, 2000). However, several authors suggested that whether behaviours should be considered as cultural depends on the type of learning process involved in its behavioural acquisition (Galef, 1992; Goodall, 1973). Indeed, it has often been argued that animal cultures differ from human ones as they mainly arise from social facilitation or local enhancement whereas human cultures arise mainly from imitation, but also from more complex processes, such as teaching or language (Boyd & Richerson, 1985; Galef, 1992; Heyes, 1993; Tomasello, 1994; Wilson, 1975).

Even if the process of social transmission matters to understand what types of cultures can be exhibited by nonhuman animals, researchers underlined the fact that terms such as teaching and imitation are problematic and can be associated either to more general or specific meanings, even with different specificity levels when applied to humans or nonhuman animals (Laland & Hoppitt, 2003). They also argued that up to date, there is no clear answer on what

makes human cultures unique (if there is such a thing as human culture uniqueness), in addition to the fact that nonhuman animals are currently judged upon stricter criteria than humans (Laland & Hoppitt, 2003). In this manuscript, we will not go further in these considerations (but see Laland & Galef, 2009; Laland & Hoppitt, 2003; Laland & Janik, 2006; Laland et al., 2009 for more details on the animal culture debate).

3) Culture or tradition?

Because of the disagreement between researchers, two terms are currently used to define group-typical behaviours that are socially transmitted: "culture" and "tradition". Some authors argue that culture and tradition should be used according to the processes leading to the emergence of the behaviour (Galef, 1992), others argue that the term tradition could be too anthropomorphic (Whiten, 2000), some consider that culture is an accumulation of traditions (de Waal, 1999, 2001) and others consider these two terms to be synonyms (Kummer, 1971; Laland et al., 2009).

4) How to test for the emergence of culture

To test for the emergence of culture in animals, researchers proposed different criteria that should be tested in order to demonstrate that a behavioural trait is culturally inherited (Danchin & Wagner, 2008, 2010; Danchin et al., 2010). For culture to emerge, social learning should result in a non-genetic inheritance of behavioural variation across generations, or at least a transmission from old individuals to young ones (Avital & Jablonka, 2000; Horner et al., 2006; Lefebvre, 1995; Whiten & Messoudi, 2008). Additionally, the phenotype of the learning individual should be modified by social learning during a sufficient amount of time for other individuals to observe and learn from its behaviour (Brooks, 1998; White & Galef, 2000). Indeed, if the social influence would only last for a short period, it would not allow a

transmission of the behaviour to younger individuals. Finally, the socially transmitted information should be generalised by individuals that would use it in new contexts, demonstrating that general rules, more than information restricted to specific situations, can be culturally transmitted (Danchin et al., 2010; Mery et al., 2009).

II) ANIMAL CULTURE

The best-known examples of animal cultures are the washing behaviour of potatoes by Japanese macaques (*Macaca fuscata*), that was observed on a Japanese island (Kawai, 1965; Kawamura, 1954), the broad repertoire of behavioural patterns in chimpanzees (*Pan troglodytes*) including tool usage (for ant-dipping, termite-fishing or nut-cracking for example), grooming (such as nasal probe) and courtship behaviours (McGrew, 1992; Whiten et al., 1999), and the piercing-behaviour of milk bottles' foil caps by several species of tits in Great Britain (great tit *Parus major*, blue tit *Cyanistes caeruleus* and coal tit *Periparus ater*; Fisher & Hinde, 1949; Figure 1).

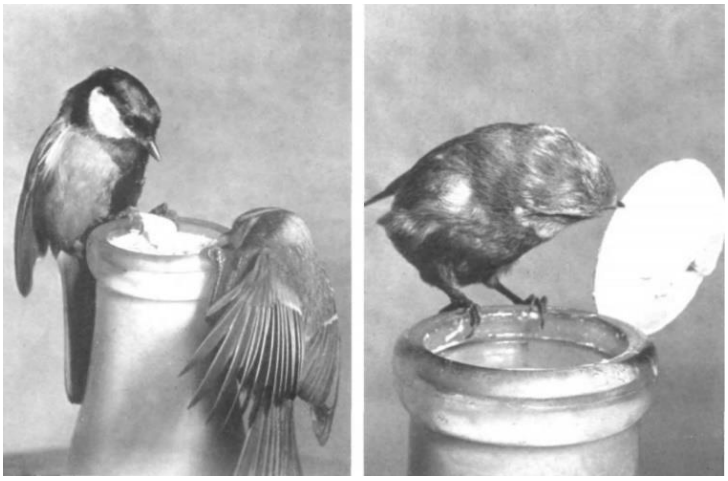


Figure 1. A famous example of animal culture: Blue and great tits opening milk bottles. From: Fisher & Hinde (1949) – Photography: V.L. Breeze. Reproduced with permission of *British Birds.*

Despite an historical disagreement over animal culture, the fact that nonhuman animals exhibit culture is now well accepted and supported by hundreds of studies demonstrating group-typical behavioural patterns among a wide range of animal taxa. I will present some examples of animal cultures, from mammals to insects.

1) Culture in mammals

a) Non-human primates

Besides the examples mentioned above, culture has also been evidenced in orangutans (*Pongo pygmaeus*): up to 24 different specialised feeding techniques (including tool use) and social signals, with distinctive local cultural repertoires across the different populations have been described (van Schaik & Knott, 2001; van Schaik et al., 2003; but see Laland & Janik, 2006). For example, in some areas orangutans use leaves to amplify their vocalisations, whereas in others, they use tools as sexual stimulants (van Schaik et al., 2003). Another example of culture in non-human primates is the one found in social conventions of capuchin monkeys (*Cebus capucinus*): five behavioural patterns that could be used to test the quality of social relationships between individuals were identified, such as sucking of body parts, hand sniffing or putting fingers in the mouth of conspecifics (interpreted as a game; Perry et al., 2003).

b) Cetaceans

Cultural behaviours have been described in cetaceans, mainly in foraging specialisation and migratory patterns (for a review, see Rendell & Whitehead, 2001; Whitehead & Rendell, 2014). In a specific population in Shark Bay, Australia, wild bottlenose dolphins (*Tursiops truncates*) use sponges to forage (Krützen et al., 2005; but see Laland & Janik, 2006), a behaviour found almost exclusively in females. Since the original study, it has been suggested that this culturally transmitted foraging technique provide access to new food items (Krützen et

al., 2014). Additionally, it has been shown that such socially transmitted specialisations in different habitats may have led to significant geographical fine-scale genetic structure, suggesting that genetic structure could be shaped by cultural transmission, as in humans (Kopps et al., 2014). Killer whales (*Orcinus orca*) also express group-typical behaviours considered as cultural (Rendell & Whitehead, 2001; Whitehead & Rendell, 2014), such as beaching themselves for foraging (Guinet & Bouvier, 1995) or knocking seals from an ice floe (Smith et al., 1981).

2) Culture in birds

In birds, a well-known example is the one found in the New Caledonian crow (*Corvus moneduloides*), a species in which individuals are able to make and use tools from sticks or Pandanus leaves (Hunt, 1996; Hunt & Gray, 2006; Rutz et al., 2007; Bluff et al., 2010b). Because geographic variation in tool design have been observed (Hunt, 2000; Hunt & Gray, 2003), this behaviour has been suggested to be a case of material culture (Hunt & Gray, 2003, 2006). Besides this famous example, other examples of bird culture that are less known are worth being presented. For example, it has been suggested that young male bowerbirds (*Ptilonorhynchidae* family) might be able to learn their bower structure and displays from active adult males (Madden, 2008), resulting in local cultures in these behavioural traits (Madden, 2008; Madden et al., 2004). Bower design and decorations differ amongst populations (Diamond, 1982, 1986, 1987) and bower decorations appear similar between close birds, which could not be explained by the availability of decoration materials in the environment (Madden et al., 2004).

More recently, an experimental demonstration of bird culture has been carried out in the study of Aplin and colleagues (2015b), who demonstrated local traditions in novel foraging techniques in wild great tits. Individuals captured in the field were trained to forage from feeders

with alternative techniques. One group of demonstrators was trained to open a puzzle box by pushing the blue side of the sliding door and the other group was trained to push the red side of it. After releasing the demonstrators in the field, the authors observed local traditions in the way that tits opened the puzzle boxes available. From only two trained birds in each sub-population, the information spread rapidly through social learning, and most birds reproduced the feeding technique that their demonstrators expressed. These local traditions were stable over two generations, despite a high population turnover, demonstrating a high social conformity between birds. Conformist transmission is defined as "the disproportionately likely adoption of the most common variant" (Morgan & Laland, 2012). Because cultural conformity is known to be a key factor in complex cultural evolution in humans (Rendell et al., 2011; van de Waal et al., 2013; Whiten et al., 2005, 2011), Aplin and collaborators (2015b) argue that their study demonstrates that complex cultural behaviours can occur in a broad taxonomic range.

3) Culture in fishes

Laland and Janik (2006) consider that one of the strongest evidence for animal culture has been found in fishes: using population translocation experiments, scientists discovered that in coral reef fishes (French grunts *Haemulon flavolineatum* and bluehead wrasses *Thalassoma bifasciatum*), schooling sites and migration routes (Helfman & Shultz, 1984), as well as routes to mating sites (Warner, 1988, 1990) were socially learned from experimented individuals. Such behavioural variation could not be explained by ecological conditions or genetics. These results show that they rather corresponded to local cultural traditions that could be maintained over multiple generations (Helfman & Shultz, 1984; Warner, 1988, 1990).

4) Culture in insects

Aside from vertebrates, culture has also been investigated in insects. For example, research on culture-like phenomena were conducted in honeybees (Lindauer, 1985). More recently it has been demonstrated that a string-pulling behaviour in order to access a reward could be culturally transmitted in bumblebees (*Bombus terrestris*), over several sequential sets of individuals ("generations"; Alem et al., 2016). Other studies showed that female mating preferences of *Drosophila melanogaster* could be learned socially (but see Auld et al., 2009 on *Drosophila serrata*) and maintained across several generations, through a high conformist bias (Bridges & Chittka, 2019; Danchin et al., 2018; Mery et al., 2009). This suggests that more animal species might express the cognitive abilities needed to successfully transmit social information across time than previously thought. This discovery in insects advocate for the fact that cultures could be an ancient evolutionary process that influenced the evolution of different taxa (Danchin et al., 2010).

5) Concluding remarks

Nowadays, with the extensive work on cultures in diverse animal taxa and in multiple behavioural contexts, it is difficult to doubt that nonhuman animal cultures do exist, explaining why this field of research has now been adopted by numerous researchers. A new question emerged following the acknowledgement of the existence of nonhuman animal cultures: how would such cultures evolve over time?

III) CULTURAL EVOLUTION

Cultural evolution can be defined as the alteration or change in a learned behavioural trait from one generation to the next. Typically, for a culture to emerge it requires three main stages: 1) innovation, often by a single individual, 2) transmission through a social network and

3) modifications at the population level (Henrich, 2001). Cultures are not static, but they are rather subject to an evolution over time, with an alteration in form, function or frequency in their component traits. Therefore, according to the way these three stages will unfold, the resulting cultures will evolve differently.

1) Assessing cultural evolution through biological concepts

Several authors suggested that cultural evolution may be assessed thought the same concepts used to describe the biological evolution (Mesoudi, 2016, 2017; Whiten et al., 2011). Accordingly, animal cultures would follow the same core concepts as genetic evolution and thereby be subject to 1) variation, selection and inheritance, 2) adaptation, 3) geographical variation and demographic processes and 4) accumulation of changes or modifications (Avital & Jablonka, 2000; Galef, 1976; Mesoudi, 2017; Mundinger, 1980; see Aplin, 2019 for a review of these concepts and their applications to birds' cultures).

a) Variation, selection and inheritance

Variation in cultural traits is often due to copy errors. For example, in songbirds, song copy errors can lead to novel song types (Lachlan & Slater, 2003). Innovations from one or several individuals are other sources of variation. For example, the potato washing behaviour of Japanese macaques is due to the innovation of a single individual: the female Imo (Kawamura, 1954). Then, a behavioural trait will be selected or not depending on the frequency at which individuals will use it, leading to different trait persistence. This process of selection will often depend on social learning biases, such as the conformist bias found in great tits (Aplin et al., 2017, 2015a, 2015b), or on the interaction between social learning and the individual's experience: for instance, in pigeons (*Columbia livia*), slight individual modifications of a socially learned flying route lead to a more effective one (Sasaki & Biro, 2017). Finally,

inheritance of cultural traits is permitted by social learning, as previously mentioned in diverse examples.

b) Adaptation

Even though the adaptive value of animal cultures is intuitive, to this date there is no experimental proof that the expression of cultural behaviours provides any survival or reproduction advantages (Aplin, 2019). In the majority of animal culture studies, culture is a source of potential adaptive behaviour, allowing individuals to find solutions to diverse problems by copying others. However, in some cases, culture also permits the transmission of maladaptive traits (e.g. smoking in humans). In animals, it has already been demonstrated that social learning could allow the spread of maladaptive information. For example, in the guppy (*Poecilia reticulata*) social transmission result in maladaptive traditions, with individuals taking a long and energetically costly route to a feeder instead of a shorter route (Laland & Williams, 1998). This transmission of maladaptive information can be due to informational cascades (Laland, 2008): individuals observe conspecifics exhibiting an arbitrary behaviour, interpret it as good because others are doing it, and start reproducing it, resulting in an arbitrary culture. For example, it has been shown that female lekking sage grouse (*Centrocercus urophasianus*) based their mating choices by relying more on mating decisions of other females than on actual male traits that could indicate his quality (Gibson et al., 1991). This led to an unpredictability of traits considered as attractive for females and a lower sexual selection (Gibson et al., 1991). In another study, using an agent-based model, authors showed that a social enhancement mechanism was sufficient to create and maintain stables traditions that could be adaptive, arbitrary but also maladaptive (Franz & Matthews, 2010).

c) Geographical variation and demographic processes

The best evidence that spatial distribution and geographic isolation can impact the form and frequency of animal cultural traits comes from passerine song studies. The colonisation of islands by songbirds provide good examples for such phenomena, with songs of island birds being different from songs of mainland birds (Baker, 1996; Baker et al., 2006). For example, chaffinches (*Fringilla coelebs*) that colonised the Chatham Islands (New Zealand) did not develop elaborate end phrases to their songs in contrast to mainland individuals. Moreover, their basic song structure did not significantly change since the colonisation around 1900 (Baker & Jenkins, 1987). Another example is the one of yellowhammers (*Emberiza citronella*) that were introduced to New Zealand and that still sing old song types that are now extinct in the native British population (Pipek et al., 2018). Within populations, immigration rates can impact the form, frequency and longevity of cultural traits such as birdsong (see Aplin, 2019). For example, in wild great tits, levels of immigration in a neighbourhood were positively correlated to the size of song repertoire (number of different song types produced by a bird) within this neighbourhood (Fayet et al., 2014).

d) Accumulation of changes or modifications

The process of accumulation of modifications is a key concept in biological evolution and has been demonstrated in human cultures through the "rachet effect": a progressive increase in the complexity and/or efficiency of technology over time (Alvard, 2003; Tomasello, 1994). However, the existence of cumulative cultures in nonhuman animals is controversial and it has been repeatedly argued that human cultures were much more likely to be cumulative than animal cultures (Boyd & Richerson, 1985; Galef, 1992, 2003). Nonetheless, the reasons that could explain this difference between human and nonhuman animal cultures are not clear (Laland & Hoppitt, 2003). One reason could be that in the wild, there are no particular

advantages to adopt a more complex behaviour when a simple one is perfectly working (Laland & Hoppitt, 2003).

One quite recent demonstration of a cumulative culture in a nonhuman animal concerns the New Caledonian crow: researchers witnessed a diversification and cumulative changes in the design of Pandanus tools and present their results as a rare case of cumulative cultural evolution in the animal kingdom (Hunt & Gray, 2003). However, this interpretation has been questioned (Bluff et al., 2010a) because there is no clear evidence for the social transmission of such tools. Indeed, even if several researchers showed that juvenile crows had opportunities to socially learn some aspects of tool making (Bluff et al., 2010b; Holzhaider et al., 2010a, 2010b; Kenward et al., 2006; Logan et al., 2016), some found genetic predispositions to use stick tools (Kenward et al., 2005, 2006), and others found correlations between tool shapes and altitudinal variation (Hunt & Gray, 2003). To date, there is no consensus on whether cumulative culture in new Caledonian crows is real or only explained by genetic and/or environmental factors (Bluff, 2010b; Laland & Janik, 2006). In addition to crows, a few other behavioural patterns might represent cumulative cultures (chimpanzees' nut cracking and Japanese macaques' sweet potato washing; Boesch, 1993, 2003) but this remains speculative (Laland & Hoppitt, 2003). Despite the criticisms, these examples suggest that the line between human and nonhuman animal cultures is fading, as more discoveries in this field are made.

2) From social learning to cultural evolution

Recently, some authors suggested that social learning could lead animal cultures to evolve in three different ways. The three resulting culture types are characterised by their stability and richness (Tchernichovski et al., 2017; Figure 2): 1) a stable monolithic culture (Figure 2A), such as the one previously described in great tits that expresses a high conformist bias (Aplin et al., 2015b); 2) a stable polymorphic culture (Figure 2B) that is best represented

by the numerous examples of vocal cultures in songbirds (that I will present later); and 3) an unstable drifting culture (Figure 2C) that can be found for example in the vocal culture of humpback whales (*Megaptera novaeangliae*) in which males within a population conform to a certain song type, but not for a very long time (Garland et al., 2011). Additionally, authors proposed a balancing mechanism between converging and diverging social forces that can shape cultural evolution (Figure 2D). For example, imitation is thought to promote the stability of culture whereas copying errors are thought to impair it (Tchernichovski et al., 2017). However, it is still difficult to know how convergence, due to imitative learning, and divergence, due to accumulation of copying errors, add up to explain the formation of local cultures (Lachlan et al., 2016). In this thesis work, I will demonstrate that such forces can influence different parts of the zebra finch (*Taeniopygia guttata*) song without preventing the establishment of vocal cultures.

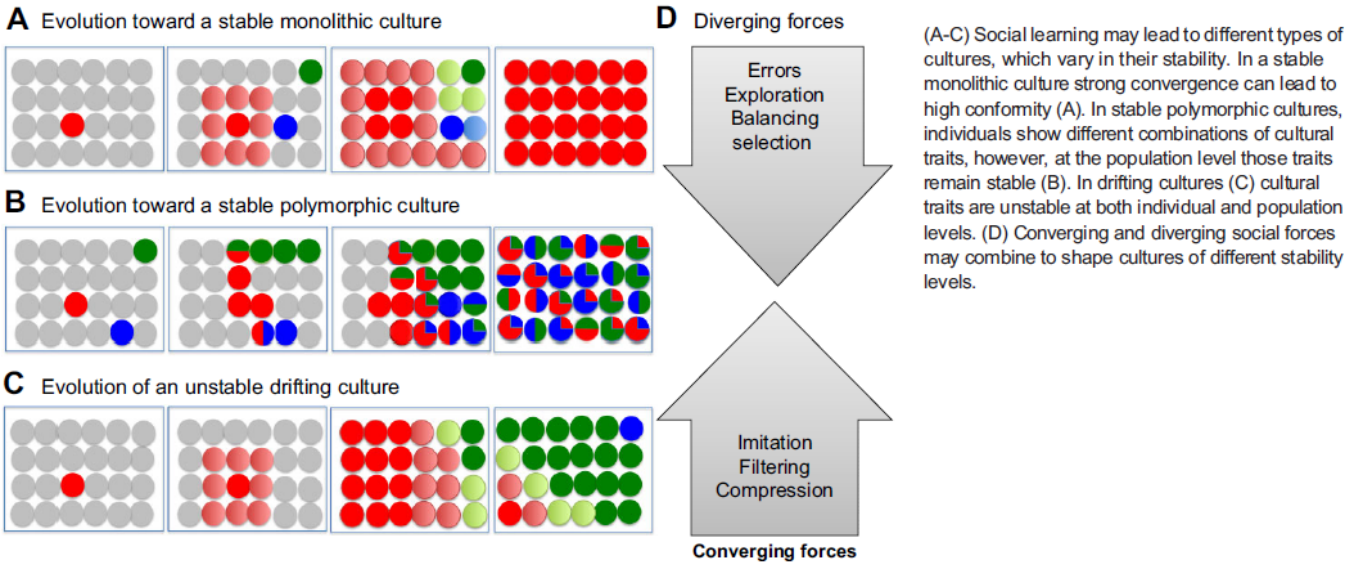


Figure 2. The evolution of three different culture types. From: Tchernichovski et al. (2017). Reproduced with permission of *Journal of Experimental Biology*.

IV) THE EXISTENCE OF VOCAL CULTURE OR DIALECTS IN NONHUMAN ANIMALS

1) Vocal learning, a prerequisite for vocal culture

Vocal learning is obviously a prerequisite for vocal cultures and can be defined as the ability to modify the form of vocal signals as a result of experience with the vocalisations of others (Janik & Slater, 2000). The ability of vocal learning is found in mammals: humans (Bruner, 1981; Hauser et al., 2002), cetaceans (Janik, 2014), elephants (Stoeger & Manger, 2014), pinnipeds (Reichmuth & Casey, 2014) and bats (Boughman, 1997, 1998); but also in three groups of birds: Hummingbirds, Psittaciformes and Passeriformes. This last group includes oscines and suboscines, with oscine songbirds representing almost half of the bird species on the planet (Bolhuis et al., 2010). Oscine songbirds effectively learn their song by imitating conspecifics (mainly adults). Thorpe (1954) conducted laboratory experiments using chaffinches and was the first to demonstrate that young birds raised in social isolation failed to produce the species' normal song characteristics. During early studies of birdsong, the first approach in which culture is simply used as a synonym for tradition appeared. At this period, titles like "The cultural transmission of birdsong" and "Cultural evolution in bird song" became common (Marler & Tamura, 1964; Catchpole & Slater, 2008). Vocal learning provides the ability to transmit sounds with high fidelity and that can potentially last for hundreds of generations (Lachlan et al., 2018). It also provides for different species as well as for different groups within the same species, the potential to develop specific vocal cultures.

2) What are dialects?

Through vocal learning, the members of a same species are able to express vocal geographical variations which are referred to as vocal dialects. The term dialect is used to define vocal variations among populations, at different geographical scales (Baker & Cunningham

1985). Vocal dialects (also referred to as "vocal cultures") have been demonstrated in a wide range of vocal learning taxa (Catchpole & Slater, 2008; Janik & Slater, 1997, 2003) including humans (Trudgill, 1983; Nettle, 1999), and constitute the largest body of evidence for cultures in the animal kingdom. Vocal dialects of nonhuman animals have been widely described in birds. But dialects have also been found in mammals, for example in bats (Boughman, 1997; Davidson & Wilkinson, 2002) and cetaceans (Ford, 1991; Rendell & Whitehead, 2001; Weilgart & Whitehead, 1997; Whitehead & Rendell, 2014).

3) Examples of vocal culture or dialects

a) Vocal culture or dialects in cetaceans

Male humpback whales can produce highly stereotyped and repetitive songs and males from different regions sing different song types (Garland et al., 2011). Within a region, all males will conform to a specific song type, but a rapid spread of song will result in a strong annual fluctuation and the males will not keep the same song type for a very long time (Garland et al., 2011). In humpback whales, the song changes gradually over the year but it can take several years to change the song entirely: for example, less than two years for Australian humpback whales (Noad et al., 2000) and more than a decade for Bermuda whales (Payne & Payne, 1985). Such vocal culture could therefore correspond to an unstable drifting culture (Tchernichovski et al., 2017).

b) Vocal culture or dialects in birds

Classically, bird vocalisations have been classified in two categories: calls and songs, even though the distinction is not always clear-cut. Catchpole & Slater (2008) describe song as “long, complex vocalizations, produced by males in the breeding season”. Calls, on the other hand, “tend to be shorter, simpler and produced by both sexes throughout the year”. However,

there are many cases where these descriptions do not fit. For example, in many tropical bird species, both sexes sing (Slater & Mann, 2004). Furthermore, recent literature surveys suggest that even in the temperate zone, song in females occurs more often than previously thought (Garamszegi et al., 2007; Odom et al., 2014). Moreover, in several species, birds may sing throughout the year even if breeding only occurs during a restricted period, for example in the Eurasian wren (*Troglodytes troglodytes,* Armstrong 1955; Cramp 1988). In birds, vocal cultures have been mainly demonstrated in the song of oscine songbirds (Catchpole & Slater, 2008; Kroodsma, 2004), but they possibly also exist in Hummingbirds (Gaunt et al., 1994; Wiley, 1971) and in calls of Corvids and Psittacids. Indeed, a study of Bluff and collaborators (2010b) suggests that in addition to possessing material culture (see above), New Caledonian crows also have vocal culture. By studying alarm calls, the authors discovered that crows exhibited significant population-level variations in those vocalisations and even though they did not identify sharp dialect boundaries, they argue that their results constitute a first step in demonstrating vocal culture in this species (Bluff, 2010b). In parrots, dialects have been widely demonstrated in contact calls (Baker, 2000; Bradbury et al., 2001; Wright, 1996; Wright et al., 2008; Wright & Dahlin, 2018; Wright & Wilkinson, 2001). Those studies demonstrate that vocal cultures can be expressed in vocal signals that are not necessarily songs, and that vocal cultures occur in a wider range of cases than previously thought during the early work on vocal dialects in songbirds. There is now a large body of evidence that vocal signals constitute cultures, especially in avian species (for a review, see Freeberg, 2000).

V) BIRDSONG DIALECTS

1) Characteristics and examples of birdsong dialects

In oscine songbirds, dialects can be defined as vocal geographical variations in the song. Many species have more than one version of their species song, called song types, and these

different versions make up their song type repertoire; but other species have only one song type (Catchpole & Slater, 2008; Podos & Warren, 2007). The work of Marler and Tamura (1962) on white-crowned sparrows (*Zonotrichia leucophrys nuttalli)* is a case study in the field of dialects in animal vocalisations. They showed that young males learned their song early in life through social learning by listening to adult males, and used the term "cultural transmission" to refer to this process (Marler & Tamura, 1964). In this species, males have only one song type and there are only few song variations between different males of the same population but great differences in the song structure of neighbouring populations (Marler & Tamura, 1962). Since then, song dialects have been described in a wide range of songbird species (for a review, see Table I in Podos & Waren, 2007; and table II in Krebs & Kroodsma, 1980) and have been established as the most widely accepted form of animal culture.

In birdsong dialects, cultural traits are stable at the population-level with birds of a same geographic area conforming to the same dialect, but individuals also show different combinations of these traits, leading to individual variations within the song that allow individual recognition (Mammen & Nowicki, 1981; Mundinger, 1970) and modulate singing interactions in territorial birds (Temeles, 1994). Therefore, birdsong dialects constitute a perfect example of stable polymorphic cultures, as proposed by Tchernichovski and collaborators (2017). However, song dialects can still vary in their stability: in some cases, song dialects can remain stable for a very long period of time, sometimes for decades (Derryberry, 2007; Garcia et al., 2015; Handford, 1988; Harbison et al., 1999; Ince et al., 1980; Trainer, 1983; Whitney, 1992) and some specific components of such long lasting dialects could even possibly last for hundreds of generations (Lachlan et al., 2018). In other cases, song dialects can quickly arise and disappear, such as in the yellow-rumped cacique (*Cacicus cela*) and the indigo bunting (*Passerina cyanea*) that modify their songs in a single year or even less (Trainer, 1989; Payne et al., 1981). Even if different temporal patterns of birdsong dialects have been demonstrated,

still little is known on the mechanisms that allow some dialects to go extinct and others to be sustained. Finally, song dialects can be distributed among different spatial scales: some dialects will be only shared by few close neighbours, constituting microgeographic song variations, whereas others will extend over thousands of kilometres, constituting macrogeographic song variations (Podos & Warren, 2007).

2) Functions of birdsong dialects

Many hypotheses have been proposed to explain the origin and maintenance of song dialects, as well as their potential adaptive significance. Some of these hypotheses that are not necessarily mutually exclusive are explained below.

a) The genetic adaptation hypothesis

This hypothesis requires that young birds are able of song production learning and song recognition learning in their natal region (Payne, 1981; Rothstein & Fleischer, 1987). Then, the genetic adaptation hypothesis (also called "local adaptation hypothesis") proposes that when adult, birds will use song dialects as a cue for assortative mating (Tomback & Baker, 1984), with females preferring to pair with males singing the locally specific variants of the song. Therefore, this phenomenon would inhibit the gene flow between the different populations of a same species and lead to local genetic adaptations (Marler & Tamura, 1962, 1964; Nottebohm, 1969, 1972). In this context, song dialects provide an adaptive function because when preferentially choosing a mate that sings the local song type, a female is ensuring that her offspring will be genetically specialised to its local habitat, with a better reproductive success and survival than foreign birds (Payne, 1981). Because this hypothesis builds on the theory of natural selection, it is highly attractive for many scientists and has been widely tested (Marler & Tamura, 1962; Nottebohm, 1969; for a review, see Podos & Warren, 2007). In a study

focusing on genetic differences among eight dialect regions of white-crowned sparrows, MacDougall-Shackleton and MacDougall-Shackleton (2001) demonstrated that song dialects were associated with reductions in the gene flow. At the same time, song dialects did not constitute strict barriers to this flow.

b) *The social adaptation hypothesis*

According to this hypothesis, populations that sing different song dialects are not thought to be genetically isolated from one another. Song dialects are rather hypothesised to constitute social markers (Feekes, 1977; Payne, 1981) that will provide advantages in a context of social and/or sexual interactions, but only for those adult males that are capable of adjusting their song behaviour to those of neighbouring birds (Payne, 1981). For example, males that share the same song types with dominant birds would have less aggressive interactions with them as well as a facility to maintain a territory and a better access to females (Payne, 1981, 1982, 1983). Similarly, song dialects could serve as markers of group membership (Feekes, 1977) and as signals of long-term residence (Rothstein & Fleischer, 1987), resulting in a reduced number of aggressive interactions between males of the same dialect group, but an increased number of aggressions toward males of foreign dialects.

Since this hypothesis was originally established, several studies confirmed that song dialects could indeed influence territorial behaviour. For example, singing male song sparrows (*Melospiza melodia*) that share parts of their repertoires can modulate and lower levels of aggression by using different kinds of vocal matching in response to the song types of their rivals during territorial disputes (Akçay et al., 2013; Stoddard et al., 1992; see Todt & Naguib, 2000 for a review of vocal matching). Furthermore, due to song dialects, birds of many species can discriminate local individuals from foreign ones, the latter of which pose a stronger threat to territory ownership (Ydenberg et al., 1988), and reduce aggression towards local individuals

(Temeles, 1994). Thus, shared repertoires within a dialect area should remain stable and polymorphic, as mentioned before (Tchernichovski et al., 2017). The stability will facilitate the retention of group identity whereas polymorphism will allow birds to signal individual identity and facilitate the possibility to modulate the vocal signal (Draganoiu et al., 2014; Tchernichovski et al., 2017).

c) The epiphenomenon hypothesis

This hypothesis proposes that song dialects do not have any adaptive significance, that they are functionless epiphenomena and simply a by-product of vocal learning (Andrew, 1962). Geographical boundaries of song dialects would thus only be due to the characteristics of the learning process (Slater, 1985). This hypothesis does not exclude that dialect groups might be genetically isolated. However, such isolation would be due to geographic barriers or founder events rather than to assortative mating. This epiphenomenon hypothesis has been defended by Slater (1985, 1986, 1989) and applied for example to the song dialects of the sage sparrow (*Amphispiza belli*, Wiens, 1982). It also has been investigated in a computer simulation model based on random patterns of song learning, that integrated varying levels of birds' mortality rate and error rate in song copying (Goodfellow & Slater, 1986). This model successfully generated a pattern of song dialects within small groups of birds, providing support for this epiphenomenon mechanism. Consequently, the authors argue that copying error rates and mortality should be accurately measured before applying any specific adaptive significances to song dialects (Goodfellow & Slater, 1986).

3) The implication of birdsong dialects in speciation

When trying to understand why Passeriformes have become the largest avian order, the hypothesis suggesting that their ability to learn their vocalisations and to form vocal dialects

have contributed to this success is very popular. Vocal traits of birds indeed provide a great model to study the possible links between divergence in vocal signals, reproductive isolation and the process of speciation (for a review on bird speciation, see Edwards et al., 2005). The importance of song dialects in birds' speciation seems to be linked to the genetic hypothesis explained earlier. In his study, Payne (1981) evoked the fact that this hypothesis could lead to a related hypothesis about the importance of geographic variation in the speciation process (Miller, 1956). However, he argues that in terms of natural selection, this process would not provide any adaptive explanation for the geographical behavioural differences, even if the geographic behavioural variation was involved in speciation (Payne, 1981). In a study of Baptista & Trail (1992), the rate of speciation was compared between birds' taxa with and without the ability of song learning. The results show only a weak correlation between vocal learning and the great diversity of species (Baptista & Trail, 1992). However, other authors argued that these results only reflected a variability in the role of song learning on reproductive divergence and present their own results suggesting that song learning could indeed impact reproductive divergence and thus promote speciation (Slabbekoorn & Smith, 2002). In a study modelling the song evolution and speciation, researchers investigated whether the cultural transmission of song could increase the rate of speciation (Lachlan & Servedio, 2004). They found that song learning did accelerate the start of the speciation process and was predicted to accelerate the speciation rate (Lachlan & Servedio, 2004). This field of research provides confidence in the fact that vocal learning successfully accelerated speciation in oscine songbirds through the emergence of song dialects within a same species and specific song cultures in different species.

VI) FACTORS ACTING ON BIRDSONG EVOLUTION

Birdsong evolution is influenced by several factors that presumably govern the cultural evolution of bird songs from one generation to the next.

1) Mechanisms of vocal learning

As mentioned earlier, song learning strongly influences the cultural evolution of birdsong through converging and diverging forces, respectively song imitation and song-copying errors/innovations (Tchernichovski et al., 2017). Indeed, it has been demonstrated that imitative song learning enables the emergence and rapid transmission of novel vocal patterns (Slabbekoorn & Smith, 2002; Slater, 1989), and that a high fidelity of song imitation promotes the stability of song dialects (e.g. Lachlan et al., 2018). For example, in brown-headed cowbirds (*Molothrus ater*), young birds copy the songs of adult males with very high fidelity, resulting in a dialect that can remain stable over 30 years (O'Loghlen et al., 2011, 2013). Even if song learning errors can act as "cultural mutations" allowing new song variants to arise (Jenkins, 1978), at the opposite it has been demonstrated that copying errors could influence the persistence of song dialects (Harbison et al., 1999).

However, vocal learning in general and birdsong learning in particular is not only shaped by the individual's experience but also by genetic constraints. For example, some birds are only capable of producing a small and simple song repertoire, such as the rufous-collared sparrow (*Zonotrichia capensis*) or the zebra finch, whereas others can exhibit large and complex song repertoires, such as the song thrush (*Turdus philomelos*) (Catchpole & Slater, 2008). Additionally, some birds considered as "close-ended learners" are programmed to learn the song only during a short period of their early lives, after which the song will be "crystallized" and further modifications of the song will be difficult (Brainard & Doupe, 2002). This is for

example the case of the white-crowned sparrow or the zebra finch. At the opposite, some birds considered as “open-ended learners” will be able to continue or restart the learning process of song when adult (Brainard & Doupe, 2002; but see Belzner et al., 2009). This is for example the case of European starlings (*Sturnus vulgaris*; Chaiken et al., 1994) or nightingales (*Luscinia megarhynchos*; Todt & Geberzahn, 2003). In this context, genetic mutations in interaction with song learning experience, could also impact birdsong evolution.

2) Sexual selection

It has been a long time since the importance of sexual selection in shaping birdsong evolution was established (Searcy & Andersson, 1986). Aspects such as the size of song repertoire, and syllable repertoire (number of distinct types of syllable sung by a male; syllables being small song units separated in time and/or structure) are generally assumed to be sexually selected traits (Searcy & Yasukawa, 1996) and their effect on females has been much studied (Catchpole & Slater, 2008). Other studies show that females may court more in response to familiar dialects than to alien dialects, such as in white-crowned sparrows (Baker, 1983; Baker et al., 1981, 1982). Additionally, several researchers demonstrated that females mated preferentially with males singing the local song type (see below).

In several species, juveniles’ vocal behaviour can actually be shaped by adult females. For example, in brown-headed cowbirds, a brood parasitic species in which youngsters are not exposed to conspecific song during early life, it has been demonstrated that males housed with females developed different song repertoires that were directly related to the song preferences of their female companions (King & West, 1983). In another study, researchers showed that females indeed communicate with males about song: females' visual displays (wing strokes) were triggered by specific vocalisations (West & King, 1988). In return, the song that elicited such displays was a very effective releaser of copulatory postures from females (West & King,

1988). Such studies demonstrate that females' responses have a biological significance and an important role in song learning. In this context, some authors also proposed that females' preferences had a great influence on the stability of vocal dialects (for reviews, see Payne et al, 1981; Baker & Cunningham, 1985; Rothstein & Fleischer, 1987). This hypothesis was supported by findings on brown-headed cowbirds. In this species, males of distinct populations exhibit different dialects that cannot be acquired by listening to adult males. Rather, it seems that females' clear mating preferences for males of their own vocal culture (Freeberg, 1996, 1998; Freeberg et al., 1999; O'Loghlen & Rothstein, 1995) lead young males to conform to the local song dialect (O'Loghlen & Rothstein, 1995, 2003). This sexual preference would thus make it adaptive for males to sing the local dialect, resulting in an important influence on dialects' stability (O'Loghlen & Rothstein, 1995, 2003).

3) Mechanics of sound production

Mechanics of sound production constitute an important factor acting on birdsong evolution. Indeed, several parameters can constrain the bird's ability to modulate the configurations of his vocal tract when singing. For example, field studies demonstrated that the beak morphology appears to influence not only the feeding behaviour, but also the singing behaviour of Darwin's finches (*Geospiza, Camarhynchus* and *Certhidea* genus; Podos, 2001; Podos & Nowicki, 2004). Beaks play a functional role in song production in songbirds, and thus, beak evolution entailed changes in the structure of finches' vocal signals: birds with larger and heavier beaks tend to produce trills with lower rates of syllable repetition and with narrower frequency range. In addition, this effect was also linked to body size: males with large beaks and body sizes exhibited a different song structure than did the small birds (Podos, 2001).

Body size is another important parameter that influences birdsong. For example, it has been shown that the variation in frequency of songs from 90 passerine species in Europe was

explained at 59% by body mass (Wallschläger, 1980). More recently, a within-species comparison in male crowned fairy-wrens (*Malurus coronatus coronatus*) showed a negative relationship between body size and song frequency, with larger males singing lower-pitched low-frequency advertising songs (Hall et al., 2013). In the context of birdsong evolution, some researchers demonstrated that the songs of several tropical birds were influenced by their body sizes: birds with large body sizes produce songs with lower emphasized frequency (Ryan & Brenowitz, 1985). However, this factor was confounded with habitat structure, larger birds living in low-forest habitats rather than in high-forest habitat (Ryan & Brenowitz, 1985). The authors suggest that body size together with evolutionary history constrained the birds' song to evolve in a way to match the sound transmission characteristics of the environment (Ryan & Brenowitz, 1985). Other studies found a correlated evolution between song and beak morphology, such as in the well-studied white-crowned sparrow in which bill size explains significant variation in song-structure over 35 years (together with vegetation density) (Derryberry, 2009). Another example in the neotropical woodcreeper subfamily (Dendrocolaptinae) demonstrated that ecological selection on beak morphology had an impact on the diversification of songs, with woodcreepers having larger beaks producing slower songs with narrower frequency bandwidths (Derryberry et al., 2012). To sum-up, extensive work on the subject of sound production mechanics proved that they indeed influence the evolution of birdsong (Derryberry, 2009; Podos & Nowicki, 2004; Ryan & Brenowitz, 1985). Additionally, it has been suggested that morphological adaptations, together with reproductive isolation, drive the evolution of vocal signals and constitute a potential cause of speciation (Podos, 2001; Podos & Nowicki, 2004).

4) Environmental factors

Environmental factors have a strong effect on the cultural evolution of birdsong. Since a long time, it is known that habitat-dependent patterns of sound transmission have a major influence on the evolution of birds' vocalisations (Morton, 1975; Bowman, 1979, 1983; Gish & Morton, 1981). Factors such as ambient noise (Ryan & Brenowitz, 1985) and vegetation density (Derryberry, 2009) can affect birdsong evolution. A study of Luther and Baptista (2010) focused on the influence of urban noise on white-crowned sparrows' dialects over a 30-year time span. They found that songs with higher minimum frequencies were favoured in the environment characterised by urban noise (louder at low frequencies) and that the dialect with the highest minimum frequency almost replaced another dialect that had lower frequency songs (Luther & Baptista, 2010). This suggests that the dialect's ability to be effectively communicated in the local environment could be one of the mechanisms that influence how dialects (and cultural traits in general) are selected and transmitted from one generation to another. This idea was originally suggested by Hansen (1979) who was interested in the link between environmental factors and the evolution of vocal learning. Several other studies focused on the influence of urban noise on birdsong (e.g. Brumm et al., 2017; Moseley et al., 2019; Slabberkoorn & Peet, 2003; Wood & Yezerinac, 2006).

Besides anthropogenic noise, other human activities can also impact the evolution of birdsong, such as anthropogenic habitat fragmentation. For example, researchers investigated the variation in vocal traditions of the Dupont's lark (*Chersophilus duponti*) and found a cultural erosion of song (i.e. an impoverishment of song repertoires) due to landscape and demographic parameters associated with habitat fragmentation resulting from anthropogenic activities (Laiolo & Tella, 2007). Indeed, as patch size, male population size and individual dispersal distance decrease, the variety of song repertoires declines (Laiolo & Tella, 2007). Similarly,

forest fragmentation leads to cultural erosion of vocalisations (lower song complexity through a decrease of syllable number and song duration) in an oscine songbird: the orange-billed sparrow (*Arremon aurantiirostris*); but not in a suboscine passerine (not capable of vocal learning): the scale-crested pygmy tyrant (*Lophotriccus pileatus*) (Hart et al., 2018). All these findings prove that environmental factors and especially anthropogenic disturbances of the environment have a major impact on the evolution of birdsong, and that they have direct implications for the conservation of biodiversity in social learning species (Hart et al., 2018; Slabberkoorn & Ripmeester, 2008).

VII) BIRDSONG AS A TRACTABLE MODEL TO STUDY CULTURAL EVOLUTION

1) The study of cultural evolution in humans and nonhuman animals

Understanding the origins and evolution of human culture and language (one aspect of culture) is challenging. Some experimental paradigms have been proposed to explain the origins and evolution of structure in human language by using a specific kind of cultural evolution called “iterated learning”: “a process in which an individual acquires a behaviour by observing a similar behaviour in another individual who acquired it in the same way" (Kirby et al., 2014). Using this paradigm, human participants were taught artificial languages and the researchers discovered that languages culturally evolved in a way to maximize their own transmissibility through an increase in language structure over time (Kirby et al., 2008). In addition, this structure was not intentional from the individuals but rather emerged as a consequence of the language transmission over time (Kirby et al., 2008).

Furthermore, the iterated learning procedure has also been used to understand the origins and evolution of cultures that were not necessarily linguistic. For example, in an experiment, participants had to immediately recall and reproduce sequences of coloured lights, and the

sequences that participants produced became the input sequences for subsequent participants (Cornish et al., 2013). Such lineages of sequences constituted an experimental simulation of cultural evolution. The authors showed that a systematic structure emerged in the light sequences, making them easier to recall (Cornish et al., 2013). They propose that this result can be assimilated to a process operating in the origins of language in humans, with cultural evolution favouring transmissible behaviours (Cornish et al., 2013).

Recent studies applied such procedures of iterated learning to nonhuman animals in order to understand human-like cultural evolution. In an experiment on baboons (*Papio papio*), researchers developed a transmission chain: a subject had to recall and reproduce the position of four red squares in a grid of 20 squares, and the behavioural output of this individual on a set of several grids was then used as the target behaviour for the next subject, and so on over 12 generations (Claidière et al., 2014). The results showed that: 1) baboons progressively increased in performance, 2) a systematic structure emerged in sets of transmission grids, with an increased number of grids in which the four red squares were connected, and 3) lineage specificity was observed, with different transmission chains converging on different distributions of grids (Claidière et al., 2014). These three aspects were long thought to be limited to human cumulative cultural evolution. In another study, Kirby and colleagues (2014) compared different methods to assess the origins of structure in language, including simulations and experiments in humans and non-humans. They hypothesise that the uniqueness of human language is due to iterated learning that rarely occur in nature, explaining why there are only few systematically structured communication systems. However, authors insist on the fact that research on the parallels between human language and birdsong are needed to validate this hypothesis (Kirby et al., 2014). Altogether, these studies provide support for the fact that experimental work on nonhuman animals could help us understand the process of cultural evolution in humans, notably the evolution of language.

2) Why use birdsong to study cultural evolution in the laboratory?

Several central questions about vocal culture that cannot be conducted on humans due to ethical reasons and due to the long time between two generations can be addressed through experiments on birds in the laboratory. Indeed, many parallels between human language and birdsong have been described (Doupe & Kuhl, 1999), such as the importance of social influences on vocal development; the importance of auditory feedback on vocal learning and maintenance; and brain lateralization regarding vocal production and perception (Bolhuis et al., 2010). As for human speech, many songbird species are subject to "sensitive" or "critical" periods of learning (Brainard & Doupe, 2002). For example, it has been demonstrated that it will be difficult for humans to learn to produce sounds of a new language by listening to a native speaker passed the early adolescence (Doupe & Kuhl, 1999). This phenomenon is similar to what is observed in songbird species considered as "close-ended learners" (Brainard & Doupe, 2002; but see Belzner et al., 2009). Many other similarities between human speech and birdsong have been found. For example, in many songbirds, as in humans, the ability of sensory learning decrease with age (see Doupe & Kuhl, 1999 for a review). Another example concerns the ontogeny of vocal production: birds start to produce early vocalisations called "subsong", which can be compared to the babbling of human infants because they are variable and generic across individuals (Brainard & Doupe, 2002).

Before being able to study the cultural evolution of birdsong, one needs to characterise features of song learning. Experimental approaches in the laboratory allowed to understand the mechanisms of song learning by focusing on the sensitive phase as well as on the importance of the song model and social interactions with it (Marler, 1970; Beecher & Burt, 2004; Brainard & Doupe, 2002). However, even if researchers inferred that similar processes of song learning happened in the wild, by using 1) data showing similarities between an individual's song and

the song of parents or neighbours (Payne & Payne, 1997; Wheelwright et al., 2008; Byers et al., 2010; Akçay et al., 2014) , and 2) knowledge on wild song dialects (Marler & Tamura, 1962; Slabbekoorn & Smith, 2002), experimental proof of song learning in the wild is scarce. A recent study used a new technique to demonstrate song learning in wild birds: they broadcasted songs with distinctive acoustic signatures (simulating vocal tutors) to young wild savannah sparrows (*Passerculus sandwichensis*; Mennill et al., 2018). The authors then present three main findings: 1) vocal learning occur in the wild: young birds learn songs by listening to simulated vocal tutors (representing adult conspecifics), 2) timing of exposure to tutor song is important: birds preferentially learn songs heard during two specific critical stages of their early life, and 3) tutored birds pass on their songs to the subsequent generation (Mennill et al., 2018). This approach provides a new way of assessing song learning in wild birds.

In contrast to song learning, most of the knowledge on cultural evolution of birdsong comes from field studies, especially from the interest in geographical song dialects and their transmission across generations (Lachlan et al., 2013; Podos, 2018). Studying cultural evolution in songbirds has many advantages but it has to be done with extreme caution and with a broad range of methods, in order to encompass all the subtleties that flow from it. To demonstrate the longevity of dialects, even those that are sung over large areas, the best way is to conduct longitudinal monitoring of populations (Williams et al., 2013; Payne, 1996). For species that have been studied for quite a long time, such as the white-crowned sparrow, a good way of measuring cultural evolution in the song is to compare historical and contemporary recordings, along with the behavioural response to these signals (Derryberry, 2011). In order to demonstrate how variability of a cultural trait such as the song has evolved, Lachlan and collaborators (2013) reconstructed the sequential colonisation of Atlantic islands by chaffinches through computational methods. They found that colonisation impacted song evolution, probably leading to a progressive loss of a species-specific feature of song (Lachlan et al., 2013).

Each measuring method should be chosen carefully, according to the question that is asked because not every technique can be applied to a particular situation. For example, one of the major problems when studying cultural evolution of birdsong in existing continental populations is that dispersal and immigration between groups of birds prevent an effective measurement of evolutionary rates of changes in birdsong (Harbison et al., 1999; Parker et al., 2012). Several alternatives can be used to counteract these types of problems. For example, experimental translocations appear useful as they allow to precisely document founder events, which is not possible for historical colonisation in island populations. Translocation methods are classically used in wildlife conservation and consist in the capture, transport and release or introduction of species from one location to another (Griffith et al., 1989; Rout et al., 2007). For example, the North Island saddleback (*Philesturnus rufusater*) originating from New Zealand was greatly endangered in the 1960s, motivating extensive translocations to several protected islands. Birdsong evolution in such translocated populations has been recently studied by Parker and collaborators (2012). They found rapid changes in birdsong that correlated with translocation history, namely that serial translocations resulted in "cultural bottlenecks" with song divergence and a reduced song variability within islands (Parker et al., 2012). Another method to study cultural evolution of birdsong while avoiding problems due to birds' dispersal is to conduct computational models. This has been done for example in the swamp sparrow (*Melospiza georgiana*): with the recording of song repertoires from 615 individuals, researchers conducted individual-based simulations and found that a high conformist bias in song learning could lead song syllable types to persist over more than 500 years, showing vocal culture with a stability that can rival those of humans (Lachlan et al., 2018). Finally, another alternative is to conduct experimentations in controlled conditions of the laboratory. One of the best case-study on the cultural evolution of birdsong in controlled laboratory conditions has been conducted on domestic zebra finches (Fehér et al., 2009).

3) A case-study for measuring cultural evolution of birdsong in controlled laboratory experiments

Zebra finches are the model of choice to study the neurobiological basis of vocal learning (Derégnaucourt, 2011). In their case-study, Fehér and colleagues examined how song culture arose in an “island colony” established by an isolate founder (Fehér et al, 2009). In a similar way to human infants deprived of linguistic input that develop only basic sounds, songbirds raised in isolation develop abnormal songs that differ from wild-type songs of the species (Catchpole & Slater, 2008). Therefore, using tutoring lineages starting from isolate founders with abnormal songs, the authors found that species-specific (wild type) song culture could emerge de novo within 3-4 generations (Fehér et al., 2009). This experiment consolidated birdsong and more specifically the song of zebra finches as a biologically tractable model of vocal culture (Fehér et al., 2009). Additionally, because song alterations accumulated over learning generations until the species-typical song culture was reached, this experiment has been considered as a rare case of cumulative evolution (or "racheting") in birdsong.

VIII) BIOLOGICAL MODEL: THE ZEBRA FINCH

1) General presentation: phylogeny, distribution, habitat, diet, reproduction, morphology and pertinence as a biological model

The zebra finch (*Taeniopygia guttata*) belongs to the Passeriformes order, the oscines (songbirds) suborder and the *Estrildidae* family. Next to the zebra finch the *Taeniopygia* genus contains only one other species. Two subspecies of zebra finches exist: the Timor zebra finch (*Taeniopygia guttata guttata*) who comes from the Lesser Sunda Islands in Indonesia, and the Australian zebra finch (*Taeniopygia guttata castanotis*) from which originates the domestic zebra finch that was studied in this thesis. This species is mainly granivorous, rarely eats insects and forages in flocks to find food resources that are patchily located in time and space (Zann,

1996). The zebra finch is considered as a highly social species that lives in loose colonies (Zann, 1996). As “opportunistic breeders” zebra finches do not exhibit seasonality in breeding (Immelmann, 1962; Zann, 1996), which constitutes a great advantage for the reproduction in captivity. Zebra finches are monogamous and form life-long pair bonds even though some extra-pair copulations can occur (Birkhead et al., 1989, 1990). They show a greater division of labour than other species: both partners build the nest, take care of youngsters (Zann, 1996) and communicate to coordinate their joint investment in parental care, in the wild (Boucaud et al., 2017) and in the laboratory (Boucaud et al., 2016). Zebra finches are tiny birds (between 10g and 17g; Zann, 1996) that present a sexual dimorphism in plumage (Figure 3).

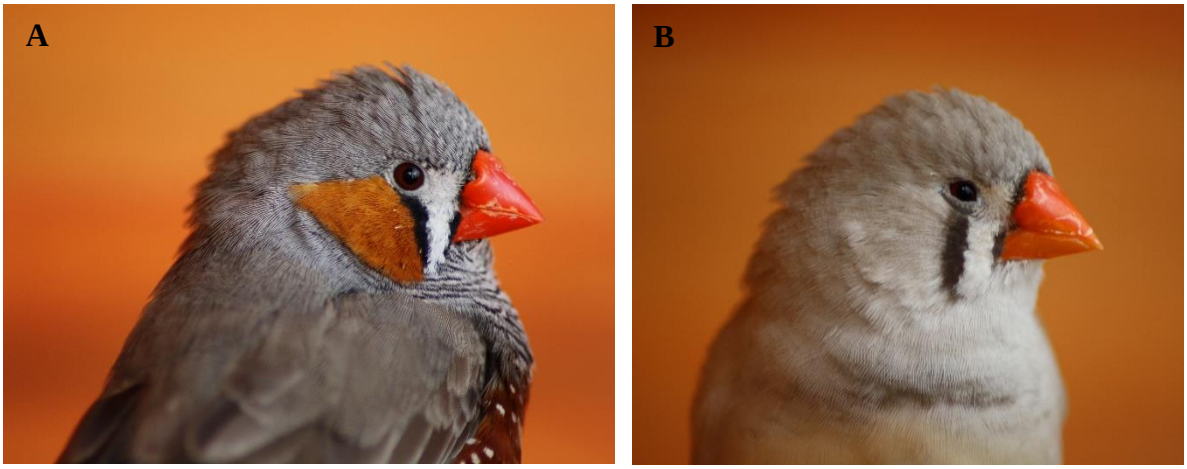


Figure 3. (A) Male zebra finch (B) Female zebra finch.
Photographies: Maurice van Bruggen – Wikimedia commons

Because they reproduce quickly and easily in the laboratory (one can expect four to five clutches per year for a pair), the zebra finch has been studied in captivity for more than 50 years and some consider it as the “flying mouse” of birdsong research (Derégnaucourt, 2011). Zebra finches are especially studied for the social and neurobiological basis of vocal learning (Derégnaucourt, 2011; Immelmann, 1962; Zann, 1996). Indeed, with his short and stereotyped song, for a long time the zebra finch has been established as a model of choice in neuroethology.

Like other oscine songbirds, the zebra finch brain comprises a network of both forebrain and brainstem nuclei that play an essential role in vocal production, perception and learning: the so called "song control system" (Nottebohm et al., 1976). Recently, technological advances such as optogenetics (Hisey et al., 2018) or online modified auditory feedback (Andalman & Fee, 2009) have provided valuable insight into our understanding of the neural control of a learned behaviour. Continuous recording of song during ontogeny (Derégnaucourt et al., 2005), together with electrophysiological recordings (Shank & Margoliash, 2009) and brain imaging (Roberts et al., 2010), revealed the influence of sleep on developmental learning. The zebra finch song was also established as a valid model to study the genetics of human speech. For example, the gene FOXP2 is essential to the development of the articulated human language and a mutation of this gene cause dyspraxia, a speech disorder. In zebra finches, knockdown of FOXP2 in one nucleus of the song control system results in an incomplete and inaccurate song imitation of the tutor (Haesler et al., 2007). In another study, Liu and collaborators (2015) used transgenic zebra finches expressing a protein implicated in Huntington's disease and responsible of the associated motor and cognitive deterioration. Those birds exhibited severe vocal disorders, a neuropathology associated with Huntington's disease and dysfunctions of the cortical–basal ganglia song circuit (Liu et al., 2015). Highlighting the parallels between speech acquisition and birdsong learning, a recent study comparing the babbling of prelingual infants with the vocal development of zebra finches shed also new lights on syllabic transitions during ontogeny (Lipkind et al., 2013). Such laboratory approaches make it possible to understand the mechanisms of vocal learning.

2) Singing behaviour

a) Song learning

In zebra finches, only males sing even though females can be induced to sing by a special sequence of hormonal treatments (Gurney, 1982). They learn to do so by listening to adult males (mainly the father) during a sensitive phase of their early life. The typical time window of this sensitive phase is between 25- and 90- days post-hatch (dph) and has been described as two specific overlapping phases: the sensory phase and the sensorimotor phase (Brainard & Doupe, 2002; Figure 4). During the sensory phase, the young bird memorises the tutor's song and during the sensorimotor phase, the bird starts the song production learning process (around 25 dph). After his scratchy first songs ("subsong" as mentioned before), the young male starts to produce "plastic song" while comparing his auditory feedback to his internal memory of the tutor's song in order to shape his final own song (Bolhuis & Gahr, 2006; Brainard & Doupe, 2002; Konishi, 1965). Past 90 dph, very few vocal changes are observed, making the zebra finch a "close-ended" learner (Brainard & Doupe, 2002; Catchpole & Slater, 2008).

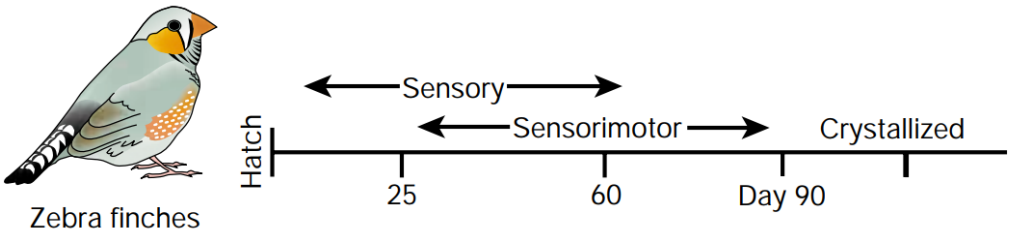


Figure 4. Timeline for song learning in zebra finches. From: Brainard & Doupe (2002). Reproduced with permission of *Springer Nature* (license number: 4694300419512).

Because zebra finches are vocal learners, they necessarily need to hear a conspecific singing in order to develop a normal song and pupils that are raised in acoustic isolation will

produce abnormal songs lacking characteristics of the species-specific song found in natural conditions (Price, 1979). The fact that social transmission is the main force driving song learning in the zebra finch is known since Immelman's pioneer study in 1969, which showed that the close interaction between a young zebra finch and the male raising him (generally the father) is the most important factor in the selection of the song model. Still, a young zebra finch can learn the song of an adult male without having any physical contact or social attachment with him (Eales, 1989). Nevertheless, both visual and vocal interaction between young zebra finches and their tutors are essential for the accuracy of song learning (Eales, 1989). This type of social transmission (from one adult to a young) is called "vertical" transmission when the song is transmitted from father to son or "oblique" transmission when the song is transmitted from an adult other than the father to a juvenile. There is also evidence of transmission between juveniles of the same generation, which is called "horizontal" transmission (Derégnaucourt & Gahr, 2013). In a recent study, Derégnaucourt and Gahr (2013) showed that a young male zebra finch that had been exposed to its father during the sensitive period of song learning, could lead a brother that had never heard the paternal song to imitate some sounds of the father. It was also demonstrated that one-to-one tutoring is the best way by which a young zebra finch could get a fairly complete imitation of the tutor's song. Operant playback is a method with which a bird can actively elicit a song playback by pecking a key or landing on a perch (Adret, 1993a, 1993b; ten Cate, 1991; Derégnaucourt, 2011; Houx & ten Cate, 1999). This active playback technique can lead to good or bad imitations, depending on the individual, but passive playback, where the juvenile has no operant control over the playback, mostly results in a very poor imitation of the song model (Derégnaucourt et al., 2013). In addition, young zebra finches can learn from multiple tutors but can also demonstrate social inhibition (Tchernikovski & Nottebohm, 1998): the more male siblings there are in a clutch, the less of the father's song is imitated. Altogether,

these studies show that song learning in the zebra finch is influenced by several social components.

Although zebra finch song is quite easy to study in laboratory conditions, it is hard to know if the extensive findings that were obtained from laboratory studies can be generalised to conditions in the wild. Indeed, groups of zebra finches are difficult to follow in the field and few studies managed to study song learning in the wild. In a field experiment, Zann attempted to determine if wild zebra finches also sung their father's song and discovered that about 65% of sons matched the songs of their respective fathers and presumably copied from them (Zann, 1990).

b) Song structure

The zebra finch song is highly stereotyped and can be described hierarchically (Figure 5). Different authors used different terms to describe similar song units in the zebra finch song (see Sossinka & Böhner, 1980; Hyland Bruno & Tchernichovski, 2017; Zann, 1996). In the following, I will describe the song with the terminology we chose to use throughout the thesis work. Typically, the zebra finch is organized from "bouts" to "elements". A song bout is considered as a period of uninterrupted singing and composed of a suite of sounds called "syllables" that are separated from each other by silent gaps (Hyland Bruno & Tchernichovski, 2017; Williams, 1990; Williams & Staples, 1992; Zann, 1996). Syllables are stereotyped and can contain a combination of different sounds with fast transitions (on a 10 ms timescale) (Derégnaucourt, 2011; Williams, 1990). A song bout is usually starting by a suite of "introductory syllables" that are followed by one or several renditions of the "motif" that can be separated from each other by a particular category of syllables recently referred to as "connectors" (Hyland Bruno & Tchernichovski, 2017; Price, 1979). Connectors resemble calls from the vocal repertoire of the species, normally produced when losing or seeking contact with

conspecifics (Hyland Bruno & Tchernichovski, 2017). The song motif is considered as the constitutive unit of the zebra finch song and consists of a short (0.5 – 1.5 s) and stereotyped sequence of syllables repeated in a fixed order (Price, 1979; Sossinka & Böhner, 1980; Williams, 1990; Zann, 1996). Finally, each syllable can be segmented into smaller units called "elements" (the smallest song unit of the zebra finch song). Elements correspond to vocal gestures (Amador et al., 2013) and are delimited by “time events”, identified as abrupt changes in amplitude or entropy (Lachlan et al., 2016; Ravbar et al., 2012).

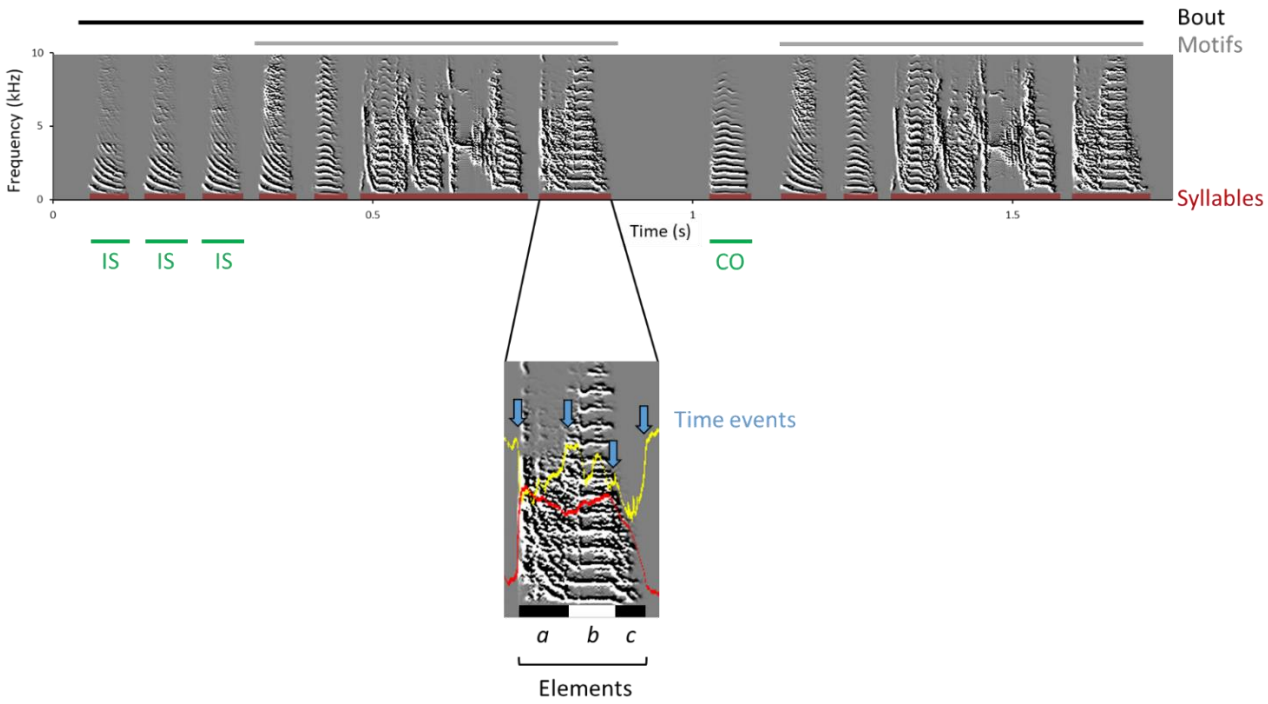


Figure 5. Spectrogram of a zebra finch song. The different units of a typical zebra finch song described above are indicated: the black bar above the spectrogram indicates the song bout and grey bars indicate motifs. Song can be segmented into distinct syllables using SAP 2011 (Sound Analysis Pro software; Tchernichovski et al., 2000); syllables being separated from each other by silent gaps and represented by red bars. Green bars under the spectrogram represent particular syllable types: “Introductory Syllables” (IS) and “Connectors” (CO). Each syllable can be segmented into elements that are delimited by time events: cursive letters from *a* to *c* indicate the different elements of the particular syllable and each blue arrow represents a different time event. The red curve represents the amplitude and the yellow curve represents the Wiener entropy. Wiener entropy is a measure of the width and uniformity of the power spectrum (noisiness of the sound).

c) Contexts of song production

As in other songbirds, young zebra finches can learn their song from more than one individual (Slater & Ince, 1979; Slater et al., 1988). The song conveys information about the bird's identity: in natural conditions, each male zebra finch sings a unique song, which constitutes an individual signature (Clayton, 1988; Cynx & Nottebohm, 1992; Williams, 1990). Zebra finches do not defend a territory. Therefore, singing behaviour is not used for territorial defense in this species. However, the song has a social function because it is used to maintain contact with conspecifics. Furthermore, it has a sexual function because it is a main feature of male courtship and female mate selection (Riebel, 2009). Male zebra finches can exhibit two types of singing: the "directed" and the "undirected" song (Sossinka & Böhner, 1980). The directed song is produced in the presence of and directed towards females and it is usually faster, more stereotyped and with less spectral variability than the undirected song (Kao & Brainard, 2006; Sossinka & Böhner, 1980). The undirected song is produced when it is not directed towards a female or another conspecific and it is thought to help strengthen pair bonds and promote flock cohesion (Immelmann, 1969; Zann, 1996). Finally, a "pupil-directed song" has recently been described in the zebra finch: tutors alter their song structure when facing a young in his sensitive phase of song learning (Chen et al., 2016). More specifically, they produce more introductory syllables and increase the duration of intervals between successive motifs compared to an undirected song, and they also modify some acoustic properties of syllables (Chen et al., 2016). Such acoustic modifications of song might help enhance the pupil's attention, thus facilitating song learning (Chen et al., 2016). For the authors, this process can be compared to "infant directed speech" in humans, i.e. when adults alter their vocalisations when speaking to infants (Fernald & Kuhl, 1987; Liu et al., 2003; cited in: Chen et al., 2016), in the same way as when humans speak to pets (Jeannin et al., 2017).

3) Females' song preferences

Female zebra finches exhibit song preferences when adult (for a review, see Riebel, 2009) and it has been demonstrated that song itself (presented without any other modality) provided enough information for females to choose a mate (Holveck & Riebel, 2007). For example, they prefer to pair with tutored males rather than with males raised in social isolation and also prefer the males from their own population rather than males with normal songs but from another population (Williams et al., 1993). Some authors suggested that these results could be due to the fact that isolated males were not able to direct song to females (Sturdy et al., 2001) but others showed that even in the absence of behavioural cues, females still preferred the tutored songs over the untutored ones (Lauay et al., 2004; Svec & Wade, 2009). It has also been demonstrated that song preferences are due to the females' early song exposure. Even if female zebra finches do not sing, they nevertheless undergo a sensitive phase in their early life during which they develop learned song preferences (Riebel, 2003). For example, untutored females prefer conspecific over heterospecific songs but are equally attracted to tutored and isolated song (Lauay et al., 2004). Additionally, females deprived of male song during the sensitive phase do not have repeatable choices when adult (Riebel, 2000). Finally, extensive work proved that adult females showed a preference for songs they heard during their early life (Clayton, 1988, 1990; Miller, 1979a, 1979b; Riebel, 2009). These studies provide support for the fact that preferences of female zebra finches could be a useful tool when investigating the dynamics of birdsong evolution: with females preferring some specific songs over others, their preference could potentially lead males' song to evolve towards a certain direction. This is also supported by the recent finding that female zebra finches could potentially guide the process of song learning in males, by giving a social feedback in response to immature vocalisations (Carouso-Peck & Goldstein, 2019).

4) Song dialects

Unlike in numerous songbird species, it has been suggested that song dialects could not arise in the zebra finch, neither in the wild nor in the laboratory. Indeed, in a detailed study on wild Australian zebra finches, Zann (1993) investigated the song structure divergence (using 31 song measurements) among 33 colonies of birds, from two different geographic zones (central and south-eastern Australia). He found that at a continent-wide scale, songs from the two distant regions could be discriminated based on these measurements (Zann, 1993). However, even though sons accurately learned their song from their fathers, there was only little song divergence between the different local populations within the same geographic area (Zann, 1993). Because movements of birds among colonies were frequent, Zann concluded that dispersal to and from colonies prevented the formation of colony-specific versions of the song in this highly social and nomadic species (Zann, 1993). More recently, a laboratory study examined an alternative hypothesis to Zann's conclusions: that imprecise song imitation prevented the establishment of local song divergence (Lachlan et al., 2016). To test this hypothesis, authors used song recordings of 13 captive populations across the world. They found some significant differentiation between populations that were not due to a genetic divergence, but with a very small effect size (Lachlan et al., 2016). Therefore, the results of this study support the idea of Zann, that local song traditions cannot emerge in the zebra finch (Lachlan et al., 2016). But in contrast to what was suggested by Zann (1993), dispersal to and from different colonies could not entirely explain the results in such captive populations, even though some laboratories might have exchanged some birds (Lachlan et al., 2016). The authors rather suggest that high rates of song learning errors led to a high within-population song diversity and prevented the establishment of long-term vocal cultures, even though populations were sufficiently isolated to allow them to diverge (Lachlan et al., 2016). Despite that both

studies present alternative explanations for such results, they agree on the fact that song dialects cannot emerge in the zebra finch.

IX) AIM OF THE THESIS

The zebra finch with his short and stereotyped song, learned during a narrow sensitive period of the early life, constitutes a perfect model to study the cultural evolution of birdsong. Therefore, using this biological model, I studied the dynamics of cultural evolution. Using a laboratory approach, this thesis is more embedded into a theoretical context of mechanisms of song learning, rather than an approach trying to reproduce what could happen in the wild.

1) Cultural evolution of birdsong in the laboratory

In chapter I of this thesis, I will describe the cultural evolution of song in three colonies of zebra finches starting with an extreme initial condition where male founders produce a very similar song: an imitation of the song model of the colony. This was achieved by exposing several males to a unique song model (song motif) during their sensitive phase of song learning, through different methods such as operant conditioning or one-to-one live tutoring with adult males. At the end of the training, the males that best reproduced the song model were chosen as founders for the colonies. In two colonies, male founders were trained with one specific song model and in the third colony, male founders were trained with a different song model. We wondered how the song would change over several generations in such an abnormal acoustic environment. With regard to previously published research, we predicted two possible outcomes: 1) either birds within a colony would vocally innovate and/or make errors in song learning and thus diverge from the original song type of the colony, which would lead to a high song diversity within each colony thus preventing the establishment of a colony-specific song type (as proposed by Lachlan et al., 2016); or 2) males would exhibit a high song conformity,

leading to the emergence of a possibly stable song dialect. Using systematic analysis of all song units of every male's song within the three colonies, we tracked changes over time and compared the colonies in their ability to form potential song dialects. In two colonies, we also performed behavioural observations of social interactions of all pupils during their sensitive phase of song learning. The purpose was to check for a potential link between such interactions and the accuracy with which young birds learned to reproduce the song model of their colony, an aspect that could have impacted the song changes within the colonies. This study provides new insights in tracking and understanding the cultural evolution of song in this model species.

2) Female preferences for the songs of their colony

In chapter II, I focused on the females' preferences. Adult females prefer the song they heard when they were young over other songs (Clayton, 1988, 1990; Miller, 1979a, 1979b; Riebel, 2009). Due to the artificial conditions created to study the emergence of dialects, during their early life, females only heard the songs of one particular dialect produced by males of their colony. In other species, song dialects can influence female mating preferences (Searcy & Yasukawa, 1996, reviewed in: Riebel, 2009). Females exhibiting a preference for male songs of their own dialect, they can possibly influence the stability of dialects (King et al., 1980; MacDougall-Shackleton et al., 2001; O'Loghlen & Rothstein, 1995; Searcy & Andersson, 1986). These findings can be interpreted in the context of the genetic adaptation hypothesis mentioned before. Thus, we wondered whether a link existed between female preference and song dialects in the zebra finch. Benefiting from the three artificial colonies and using an operant task with song as a reward, we tested whether females would prefer a song similar to what they had heard during their early life within their colony, to a zebra finch song different from their colony song type. Our prediction was that females should prefer songs that resemble those produced by males of their colony.

3) Song as a mediator for social learning

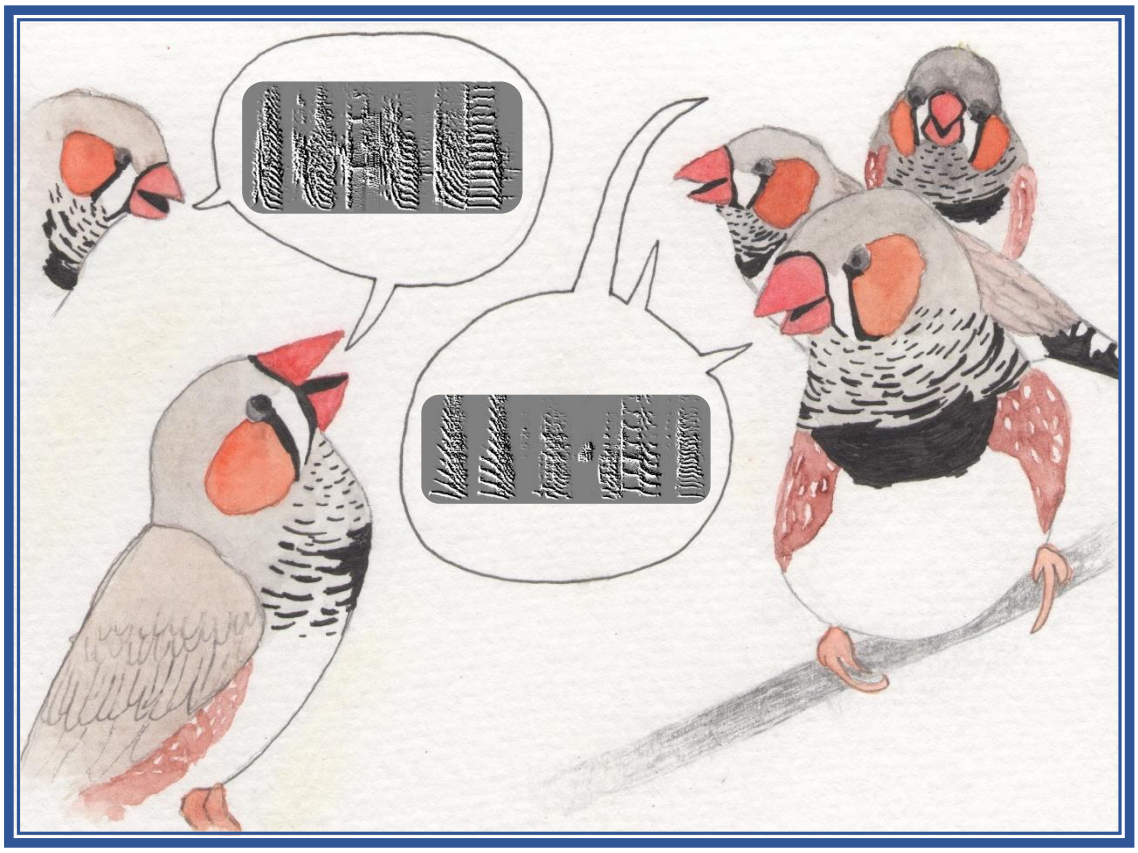
Finally, chapter III focuses on the impact of song on social learning in zebra finches. Song dialects can signal group identity (Briefer et al., 2008; Hausberger et al., 2008) and could potentially increase group cohesion in social birdsong species (Hausberger et al., 2008). If this is the case in the zebra finch, the type of song should have an impact on a birds' social learning. Due to their ecology and highly social behaviours, social learning of food choice appears as an adaptive strategy for zebra finches. Indeed, using classical observer-demonstrator paradigms (Galef, 1988), several studies showed that zebra finches were capable of social learning about foraging (Benskin et al., 2002; Guillette & Healy, 2014; Katz & Lachlan, 2003; Riebel et al., 2012; Rosa et al., 2012). Hence, they provide a good model to investigate which factors can affect social learning preferences. Several factors have already been tested, such as sex (Benskin et al., 2002; Guillette & Healy, 2014; Katz & Lachlan, 2003), familiarity (Benskin et al., 2002) and postnatal environment (Riebel et al., 2012). However, no studies focused on the effect of song on social learning. Therefore, using a methodology consistent with these earlier studies, we investigated whether male and female observers would be more likely to copy the food choice of an individual singing their colony song type or an individual singing a different song. If the song truly represents a group signature in this species, we predicted that birds of both sexes would preferentially learn from a demonstrator singing their own dialect, and this, regardless of which colony he or she originated from.

The aim of this thesis is to provide a better understanding of the dynamics of cultural evolution of communication signals, an important topic in human language research. In addition, this work presents multidisciplinary aspects since the study of birdsong is of interest in different fields such as linguistics (cultural transmission of vocal traits), evolutionary biology

(functions of vocalizations and evolution of vocal culture), neuroscience (neural basis of vocal production and perception) and physics (signal processing).

⁎ Chapter I ⁎

Towards artificial song dialects in the zebra finch



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Towards artificial song dialects in the zebra finch

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SUMMARY

In humans and other animals, several behaviours are transmitted through social learning and are considered as cultural traits. In oscine songbirds, vocal learning allows the possibility to transmit sounds with high fidelity, leading to the establishment of geographical variations in song called dialects and considered as vocal cultures. In the zebra finch, only weak populational song variations have been found. In wild populations of this species, frequent exchanges between groups of birds probably prevent the formation of local song dialects whereas in domesticated populations, frequent learning errors could favour within-population variability. The zebra finch song has been established as a tractable model of vocal culture in the laboratory. Therefore, we studied cultural evolution of song in three different colonies founded by birds trained to produce the same song motif, considered as the song model. The motif is the main constitutive unit of song in this species and is composed of a stereotyped sequence of sounds repeated in a fixed order; song being produced in bouts composed of the repetition of several motifs sometimes separated by other call-like sounds. We found that most males hatched in those colonies conformed to the original song model, but they introduced some variability at the macrostructural level of song, namely the song bout. We also observed that acoustic specificities emerged in each colony, a phenomenon reminiscent of vocal dialects. Behavioural observations confirm that young males do not necessarily affiliate with or vocally learn from adult males more than from other conspecifics. Altogether, our results suggest that song dialects can arise in artificial conditions in this species considered as the birdsong model of reference in neuroethology. They pave the way to study the roots of the socio-sexual components linked to dialect formation such as female preference for local songs and the use of vocal sharing for both population organization and decision making.

Keywords: birdsong learning, dialect, zebra finch, social interactions, vocal culture

CHAPTER I

INTRODUCTION

In humans and other animals, group-typical behavioural patterns that are shared by members of communities and are to some degree reliant on socially learned and transmitted information, can be considered as cultures (Laland & Janik, 2006). Some examples of animal culture are famous such as the potato washing behaviour in Japanese macaques (*Macaca fuscata*, Kawamura, 1954) or the opening of milk bottles in great tits (*Parus major*, Fisher & Hinde, 1949). More recently, new foraging techniques have been experimentally induced to study local traditions in wild great tits across generations (Aplin et al., 2015).

Oscine songbirds learn to sing by imitating mainly their conspecifics and birdsong has been established as a biologically tractable model of culture (Fehér et al., 2009). Vocal learning, an important component of language, allows both the possibility to invent new sounds, together with transmitting sounds with high fidelity. Such a capacity accelerated speciation in oscine songbirds (Lachlan & Servedio, 2004), by enabling distinct vocal geographical variations also called dialects (Marler & Tamura, 1962). Several studies have shown that these song dialects remain stable over time, sometimes over decades (Derryberry, 2007; Trainer, 1983; Harbison et al., 1999; Garcia et al., 2015; Whitney, 1992; Lachlan et al., 2018). In such stable polymorphic cultures, vocal traits are stable at the population-level, whereas individuals show distinct combinations of these traits (Tchernichovski et al., 2017), allowing individual identification (Mammen & Nowicki, 1981; Mundinger, 1970). Such individual variation allows individual recognition that can modulate singing interactions in territorial birds (Temeles, 1994). Both converging and diverging social forces shape birdsong dialects; the main converging force being song imitation whereas the diverging forces being song-copying errors and innovation (Tchernichovski et al., 2017). In large populations, slight copying errors could result in quantitative changes of the song, acting as “cultural mutations” and influencing the

persistence (Harbison et al., 1999) and the emergence (Jenkins, 1978) of dialects. However, other factors can impact birdsong evolution, such as sexual selection (Searcy & Andersson, 1986), biomechanic aspects of sound production (Podos & Nowicki, 2004) and environmental factors such as urban noise (Brumm et al., 2017) or other acoustic properties of the environment such as habitat structure (e.g. Boncoraglio & Saino, 2007; Ey & Fischer, 2009).

Our understanding of vocal imitation in songbirds comes from two approaches, with laboratory experiments mainly focusing on the sensitive phase of song learning and the importance of the song model, whereas field studies mostly highlighted the existence of geographical song dialects and their transmission across generations (Lachlan et al., 2013; Podos, 2018). However, a recent study merged these two approaches by using a controlled song-learning design for birds living in the wild (Mennill et al., 2018). By broadcasting songs of experimental tutors through loudspeakers to savannah sparrows (*Passerculus sandwichensis*) from birth to adulthood, the authors provided the first direct experimental evidence that wild birds learn to sing based on sounds heard early in life. Furthermore, birds passed such experimentally acquired songs to subsequent generations (Mennill et al., 2018). Although most studies about cultural evolution of birdsong are based on field recordings, the song of the domestic zebra finch (*Taeniopygia guttata*) - the model of choice to study the neurobiological basis of vocal learning (Derégnaucourt, 2011) - has been established as a tractable model of vocal culture in the laboratory (Fehér et al., 2009). This tiny bird is a highly social species that breeds easily in captivity. Only males sing and young males learn their song by imitating the song of conspecifics, mainly adults, during a sensitive period of their early life, between 25- and 90-days post-hatch (dph). Few vocal changes are observed thereafter (Immelmann, 1969). Young male finches raised in acoustic isolation from adult males during the sensitive period produce song with characteristics that differ from wild type song found in laboratory or natural colonies (Price, 1979). Using tutoring lineages starting from isolate founders, Fehér et al. (2009)

observed that juveniles imitated the isolate tutors, but song alterations accumulated over 3 to 4 generations, demonstrating that species-typical song culture can appear *de novo*. Data accumulated both in the field and in the laboratory suggest that dialects do not emerge in the zebra finch (Lachlan et al., 2016; Slater & Clayton, 1991). Nevertheless, song variations, even if they are weak, have been evidenced in the wild. Zann (1993) observed some differences in the song of different Australian populations but he concluded that dispersal to and from colonies prevented the formation of colony-specific versions of the song in this highly social and nomadic species. A recent study on captive populations of domesticated zebra finches suggests that a high rate of learning errors prevent the establishment of song dialects (Lachlan et al., 2016).

Under natural conditions, each male zebra finch sings a different song, which constitutes an individual signature (Clayton, 1988; Cynx & Nottebohm, 1992; Derégnaucourt, 2011; Forstmeier et al., 2009). In our study, by using controlled laboratory conditions, we succeeded to select males that all produced imitations of the same song model. Those males were used as founders of artificial colonies. In this artificial situation, we predicted two opposite possible outcomes: 1) a high conformity of the song between individuals if young males that hatched in the colony produced a faithful imitation of the song model that could lead to a stable song dialect; 2) at the opposite, a high amount of vocal innovation and copying errors of the song model could lead to major inter-individual song variation. Such variation would lead to an unstable drifting culture and prevent the emergence of a song dialect (Lachlan et al., 2016).

RESULTS AND DISCUSSION

The zebra finch song is hierarchically organised: the motif is defined as a short and stereotyped sequence of syllables separated from each other by silent gaps; each syllable being composed of one or several fine-grained units called “elements”, which correspond to vocal

gestures (Amador et al., 2013). Using an operant playback procedure, we trained young male finches to imitate the same song motif (Derégnaucourt et al., 2013): the song model A (Figure 1A). Using a procedure to calculate similarity between the song model and its imitation (Tchernichovski et al., 2000), we kept only those males that produced a close-to-perfect-copy of the song model (mean similarity ± SD = 95% ± 4). We used two of them to train other young males in one-to-one tutoring: this procedure guaranteed a faithful imitation of the tutor's song (Derégnaucourt et al., 2013). Ten males that produced a very good copy of the song model were used as founders of a first colony (hereafter referred to as colony A1). These males were transferred in an aviary with ten females without sexual experience that have been raised in the absence of adult males to avoid any imprinting on male song (Riebel, 2003). Two founder males died before any pupils hatched, leaving us with eight founder males. After 400 days of experiment, a total of 48 males had been hatched in colony A1.

Following colony A1, we subsequently created two other colonies. To check whether the number of founders could have an impact on the cultural evolution of birdsong, we created a second colony (hereafter referred to as colony A2) with only three males that hatched in colony A1. These males were selected based on their similarity to the original song model A. To check whether the acoustics of the particular model chosen for these two colonies could also have an impact on the results, we used three founder males that were trained with a different song model (song model B; Figure 1A) to create a third colony (hereafter referred to as colony B). In the same way as for colony A1, founder males of colony A2 and B were introduced to aviaries with naive females and could reproduce freely. After 400 days of experiment, a total of 34 males had been hatched in colony A2. In colony B, we obtained a total of 35 males during 555 days of experiment. To compare the results with those of wild type song of domesticated zebra finches, we used recordings from another group of birds (hereafter referred to as "group

C", n = 24) with the same genetic background as the birds of the three colonies, but raised in standard aviaries without any attempt of selection based on their songs.

Changes of the similarity to the song model over time

The first aim of our study was to examine whether birds that hatched in the three artificial colonies conformed to the song model or deviated from it. To do this, we first focused our analysis on the core motif of the males' song, defined as the largest repeated song unit that could be traced back to the song model of his colony (Figure S1). Using SAP 2011 (Sound Analysis Pro software; Tchernichovski et al., 2000), we calculated a similarity score between each offspring's core motif and the song model of his colony. We observed some inter-individual variability in the similarity scores: some males produced a very good copy of the song model while others emitted a poor copy of the model (Figure 1A). Despite this variability, in colony A1, most of the males produced a rather similar version of their original song model (mean ± SD = 82% ± 16). Furthermore, some late-hatched pupils produced a very good imitation of their song model (Figure 1B). We found the same results in colony A2 and colony B: most of the males produced a rather similar version of their original song model (colony A2 = 75% ± 14; colony B = 87% ± 9). Furthermore, some late-hatched pupils produced a very good imitation of their song model (Figure 1C & 1D). Overall, the similarity to the song model decreased over time in the three colonies: this decrease was significant for colony A1 (r_s = -0.573, $p < 0.001$, Figure 1B) and B (r_s = -0.592, $p < 0.001$, Figure 1D), but not for colony A2 (r_s = -0.288, $p = 0.098$, Figure 1C). This indicated that the core motif tended to change over time in the three colonies.

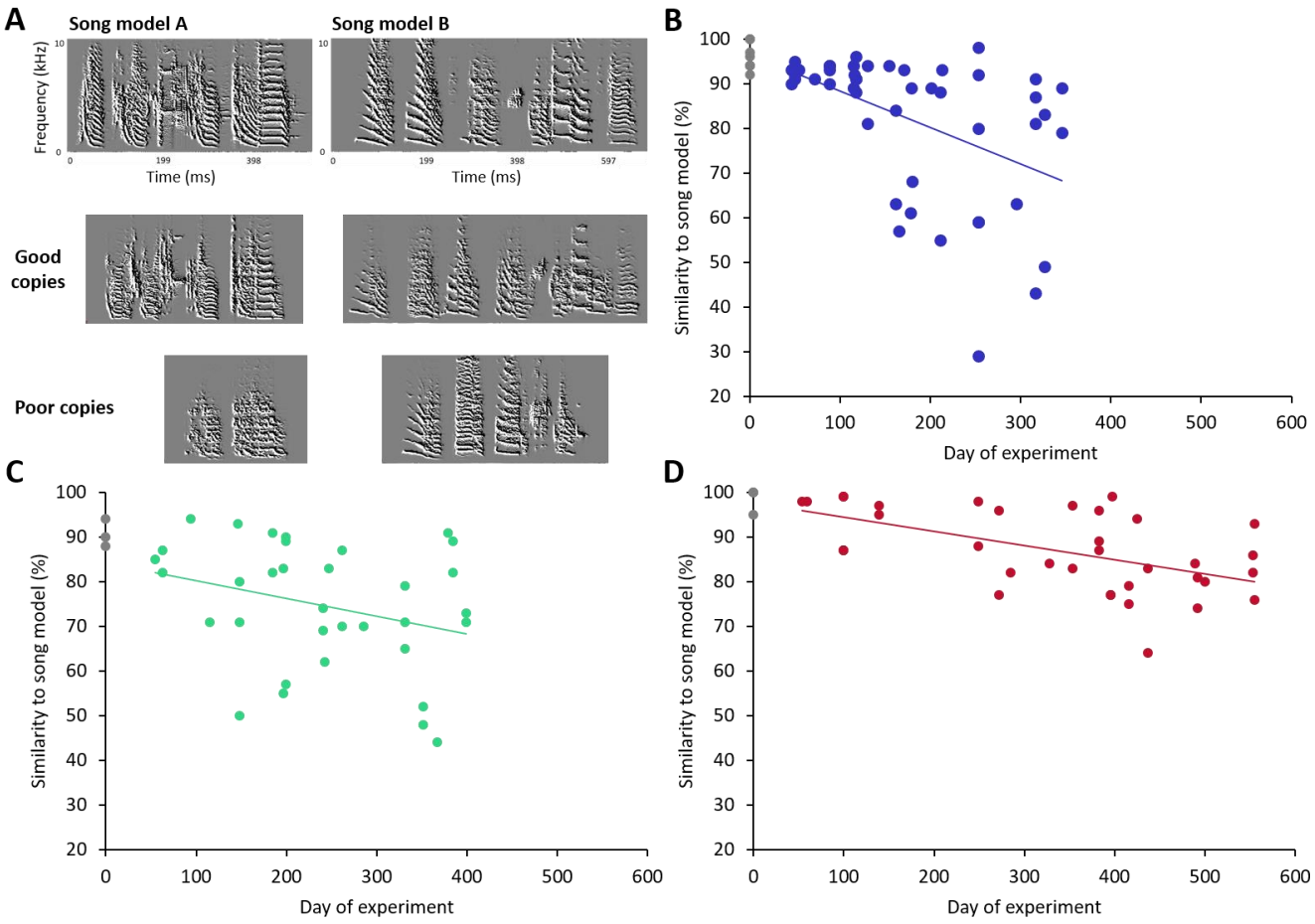

Figure 1. Imitation of song models in three colonies of zebra finches.

Overall similarity to the song model decreased over time but some late-hatched pupils produced a very good copy of the song model in the three colonies.

(A) Spectrograms of song model A and B and one example of a good and a bad copy for each song model.

(B) Similarity to song model A significantly decreased over time in colony A1 (r_s = -0.573, $p < 0.001$).

(C) Similarity to song model A decreased over time in colony A2, but this decrease was not significant (r_s = -0.288, $p = 0.098$).

(D) Similarity to song model B significantly decreased over time in colony B (r_s = -0.592, $p < 0.001$).

In panel (B), (C) and (D), grey dots represent founder males. On the *x*-axis, each male is represented according to his hatching day in reference to the day of the experiment, day 0 of the experiment being the day when male founders were introduced into the aviary with naive females.

Inter-individual variability in the song bout structure

The song of the zebra finch is hierarchically organized from motif to elements. On a higher level, the song of the zebra finch is produced in bouts; each bout usually starts with syllables called “introductory syllables”, followed by one or several renditions of the motif, sometimes separated by syllables recently referred to as "connectors" (Hyland Bruno & Tchernichovski, 2017, Figure S1). Those connectors usually resemble calls from the vocal repertoire of the species, especially calls produced to keep or establish contact with conspecifics. Using SAP 2011, we segmented as many song bouts of each male until we obtained 300 syllables per male. After having segmented song bouts into syllables, we categorized each of these sounds as following: 1) introductory syllable; 2) connector; 3) motif syllable (Figure S1).

We observed a high variability in the different types of connectors produced by birds: there was an intra-individual variability (some individuals produced different types of connectors) together with an inter-individual variability both within and between the different colonies (Figure S2). Additionally, we found a high inter-individual variability in the mean number of connector types produced per song bout by pupils of colony A1 (2.47 ± 1.46): some birds did not use any connectors between successive motifs, whereas others produced several connector types in their song bouts (Figure 2A). We found similar results in colony A2 and B (mean number of connector types produced per bout ± SD: colony A2 = 3.14 ± 1.61; colony B = 1.40 ± 0.79; Figure 2B & 2C), even though pre-existing inter-individual variability in founder males was lower in colony A2 and B than in colony A1 due to the reduced number of founders (three male founders in A2 and B versus eight in A1). This was particularly the case in colony B since all founders exhibited a simpler song bout structure, with a mean number around 1 connector type between two motifs within a song bout (Figure 2C).

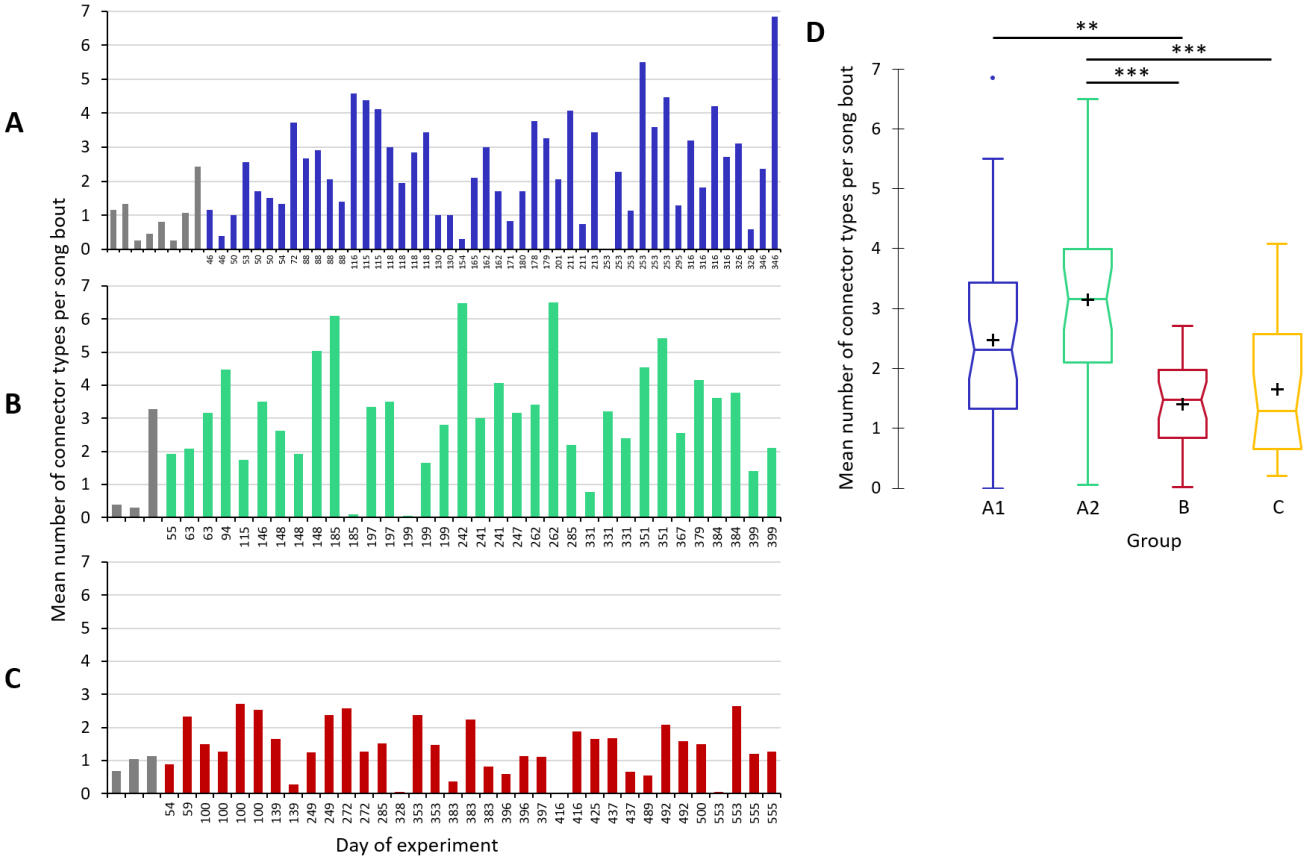

Figure 2. Song bout structure exhibits a high inter-individual variability

(A), (B) and (C): Mean number of connector types per song bout over time in colony A1 (A), colony A2 (B) and colony B (C). Grey bars represent the founder males. On the *x*-axis, each male is represented according to his hatching day in reference to the day of the experiment, day 0 of the experiment being the day when male founders were introduced into the aviary with naive females.

(D) Significant group differences in the mean number of connector types per song bout ($F = 12.2$, $df = 3$, $p < 0.001$, see Table S4). Box-and-whisker plots depict the median, interquartile range and non-outlier range (whisker length up to 1.5 times the interquartile range). Crosses indicate mean values.

The mean number of connector types produced per song bout constitutes one possible metric of the song bout structure. But because some variability arose in the song bout structure of birds in the three colonies through the variable number of connector types, we assumed that this might have influenced other metrics of song bout structure that represent how much a song is stereotyped. To quantify such song stereotypy in the three colonies, we used three well-

established measures: linearity score, consistency score and stereotypy score (Scharff & Nottebohm, 1991; Iyengar & Bottjer, 2002; Kao & Brainard, 2006; Zevin et al., 2004; see STAR Methods). The linearity score represents how often syllables are sung in a specific order. The consistency score represents how often specific variations of the song bout occur. In other words, it does not represent how syllables are ordered but the amount of time a particular sequence of syllables is sung. The overall stereotypy in the song is represented by the stereotypy score, which is the mean of linearity and consistency scores. We did not find any significant changes of these scores over time in the three colonies (Table S1).

Song analysis at the syllabic and the sub-syllabic levels

After investigating the macrostructural level of song organization, we expanded our song analysis by looking into details at the syllabic and sub-syllabic level of song. At the syllabic level, we tracked the changes of syllable duration over time in the three colonies, by calculating the mean syllable duration over 300 syllables per male. In colony A1, we found a significant decrease of syllable duration over time (r_s = -0.321, p = 0.026, Figure S3A). However, this was not the case in colony A2 and B (colony A2: r_s = -0.227, p = 0.195; colony B: r_s = -0.295, p = 0.085, Figure S3B & S3C). This may indicate that the process of change within the song (firstly seen at the core motif level) had not the same impact on syllables in the three colonies.

As mentioned earlier, syllables can be segmented into fine-grained units called “elements”, which correspond to vocal gestures (Amador et al., 2013; Figure S1). Using amplitude and Wiener Entropy, we detected abrupt changes in these measures in order to segment each male’s core motif into elements. The segmentation of syllables and elements in SAP 2011 allowed us to extract 13 acoustic parameters for each segmented song unit (for details see section “song analysis” in STAR methods). In order to check whether some sounds could

be specific to a particular colony or to a particular song model at the syllabic and sub-syllabic level, we performed a clustering analysis on syllables and elements. Syllables and elements were clustered based on the 13 song parameters measured using SAP software. We used a clustering method based on Bayesian Gaussian Mixture models (BGM, Lachlan et al., 2016). Using this method, we obtained 26 syllable clusters (Figure 3A). Over these 26 syllable types, the same 25 clusters were found in colony A1 and A2, 20 clusters were found in colony B and 21 in group C (Figure 3C; Table S2). Syllables clusters were used at different frequencies of occurrence in our four different groups (χ^2 = 46435, df = 75, $p < 0.001$, Figure 3C). However, we noticed that colony A1 and A2 were closer to each other in terms of cluster types repartition than with the other groups (Figure 3C). To investigate whether sound clusters might be affected by the specific song model rather than the colony, we considered only three groups, one per song model: group A (song model A, i.e. colonies A1 and A2 combined), group B (song model B, i.e. colony B) and group C (wild type song, individually different song models). We quantified the percentage of occurrence of each cluster in these three groups and considered that one cluster was specific to one song model (to one group) if at least 75% of these cluster's occurrences were found in one of the three groups. We confirmed this criterion by visually reviewing the sonograms of each syllable and element clusters. We found 9 syllable clusters that were specific to the song model A, with one of them (cluster 15) exclusively present in the song model A (Figure 3E). Two syllable clusters (cluster 1 and 25) were found to be sung specifically in group B and one syllable cluster (cluster 3) was exclusively produced in group C (Figure 3E). These specific syllable types are overlined in Figure 3A.

The clustering analysis on elements resulted in a total of 15 clusters (Figure 3B). All of them were found in colony A1, 14 in colony A2 and B and the 15 clusters were found in group C (Figure 3D; Table S2). As for syllable clusters, element clusters were used at different frequencies of occurrence in our four different groups (χ^2 = 810.56, df = 42, $p < 0.001$, Figure

3D). However, colony A1 and A2 had a very similar cluster types repartition compared to the other groups (Figure 3D). Regarding the song model, we found that four types of elements were specifically sung in group A (clusters 4, 5, 11 and 14), one was specific to song model B (cluster 9) and none to group C (Figure 3F). These specific element types are overlined in Figure 3B. Altogether, these findings reveal that each song model led to the establishment of a specific repertoire of syllable and element types.

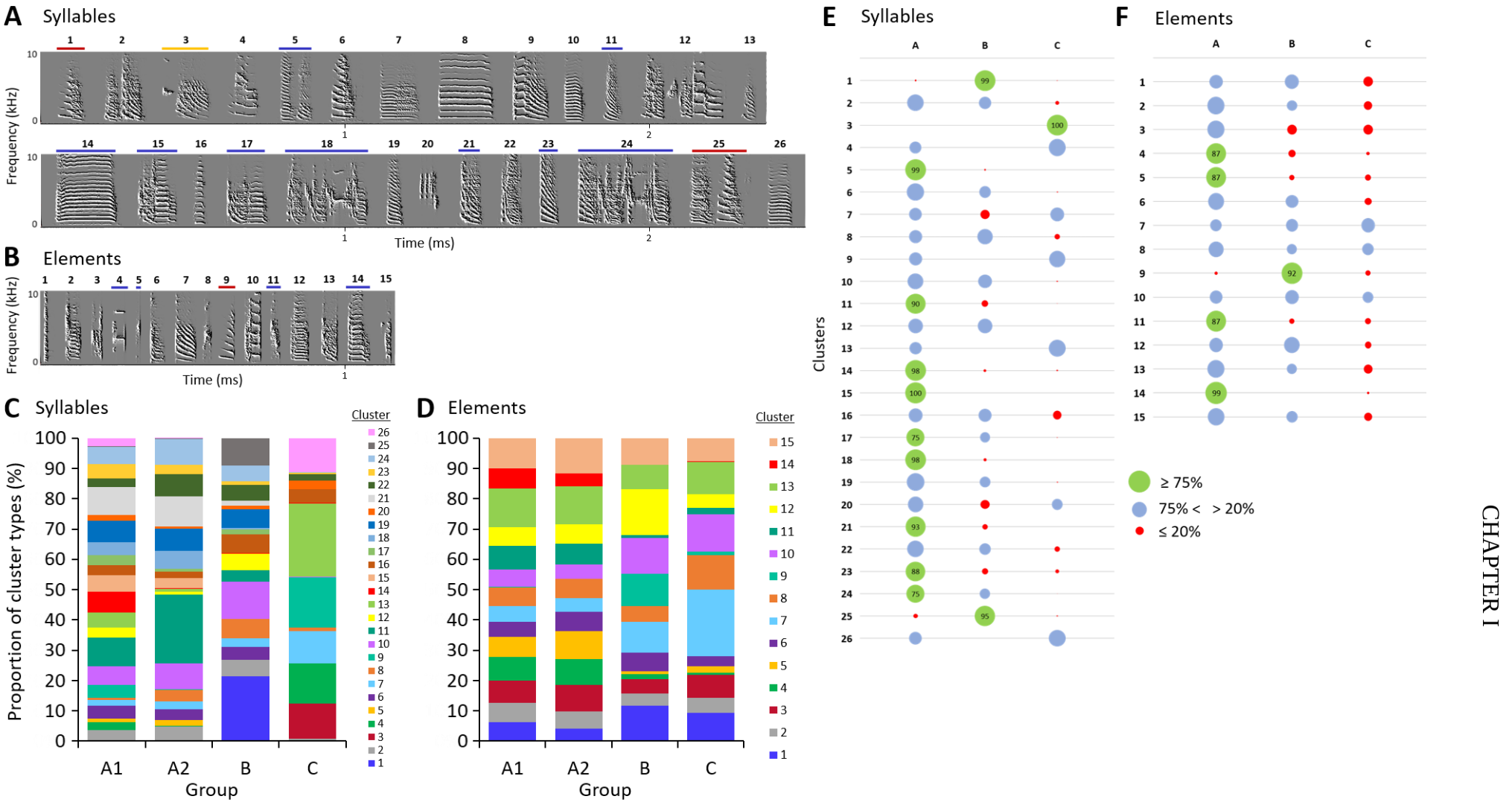

Figure 3. Some syllables and elements are specific to a particular colony or song model

(A) and (B): Examples of syllable clusters (A) and element clusters (B).

In panel (A) and (B), clusters that are specific to one song model (one group) are overlined: in blue for specific clusters of group A (song model A, i.e. colonies A1 and A2 combined), in red for group B (song model B, i.e. colony B) and in yellow for group C (wild type song, individually different song models).

(C) and (D): Proportions of syllable (C) and element (D) cluster types in each of the four groups. The frequencies of occurrence of syllable clusters ($\chi 2 = 46435$, $df = 75$, $p < 0.001$) and element clusters ($\chi 2 = 810.56$, $df = 42$, $p < 0.001$) differed between the four groups.

In panel (C) and (D), colour labels refer to the cluster types showed in panel (A) and (B).

(E) and (F): Proportions of syllable (E) and element (F) cluster types in each of the three groups representing the song models: group A = song model A; group B = song model B; group C = no uniform song model. Circle sizes are relative to the percentage of syllable (E) and element (F) occurrences in each cluster. Green circles represent a percentage over or equal to 75%, blue circles represent a percentage between 20 and 75% and red circles represent a percentage below or equal to 20%. 20%.

We looked at the dynamics of these syllable and element clusters over time in the three colonies. Most of the syllable and element types were already present in the song repertoire of the male founders. In colony A1, 21/25 syllable types and 15/15 element types were already produced by the founder males. In colony A2, 21/25 syllable types and 14/14 element types were already produced by the founder males. And in colony B, 13/20 syllable types and 13/14 element types were already produced by the founder males (Table S2). We then investigated whether the use of these clusters by birds of the three colonies changed over time. We calculated the percentages of produced clusters in the repertoire of each male, and found that, in the three colonies, there was a high inter-individual variability in how syllable and element types were used: some males used a higher amount of syllable and element types than others, regardless of their hatching date (Figure S4). Concerning the use of syllable clusters, we found a significant decrease in their production over time only in colony A1 (r = -0.354, p = 0.0137): males used less and less different syllable types. This was not the case in colony A2 and B (colony A2: r = 0.134, p = 0.451; colony B: r = 0.0853, p = 0.623). As previously suggested with the results concerning syllable duration, this may indicate that the process of change within the song did not impact the syllabic level uniformly in the three colonies. However, in colony A1 and A2, we observed a significant decrease in the production of element types over time (colony A1: r_s = -0.45, p = 0.0015; colony A2: r = -0.34, p = 0.04). That was not the case in colony B (r_s = -0.142, p = 0.412). This again showed that the song core motif changed over time, and together with the results concerning the significant decrease of the similarity score to the song model, this finding suggests that the song core motif tended to simplify over time, with males using fewer and fewer element types.

To confirm the hypothesis of a decrease in the number of element types, we verified whether the absolute number of elements per core motif changed over time. We indeed found that the overall number of elements per core motif slightly decreased over time in the three

colonies (colony A1: r_s = -0.484, p < 0.001; colony A2: r = -0.382, p = 0.026; colony B: r_s = -0.429, p = 0.01, Figure 4A, 4B & 4C). This was the case despite the fact that some males produced additional elements compared to the model (model A was originally composed of 15 elements and model B of 19) and compared to the founder males.

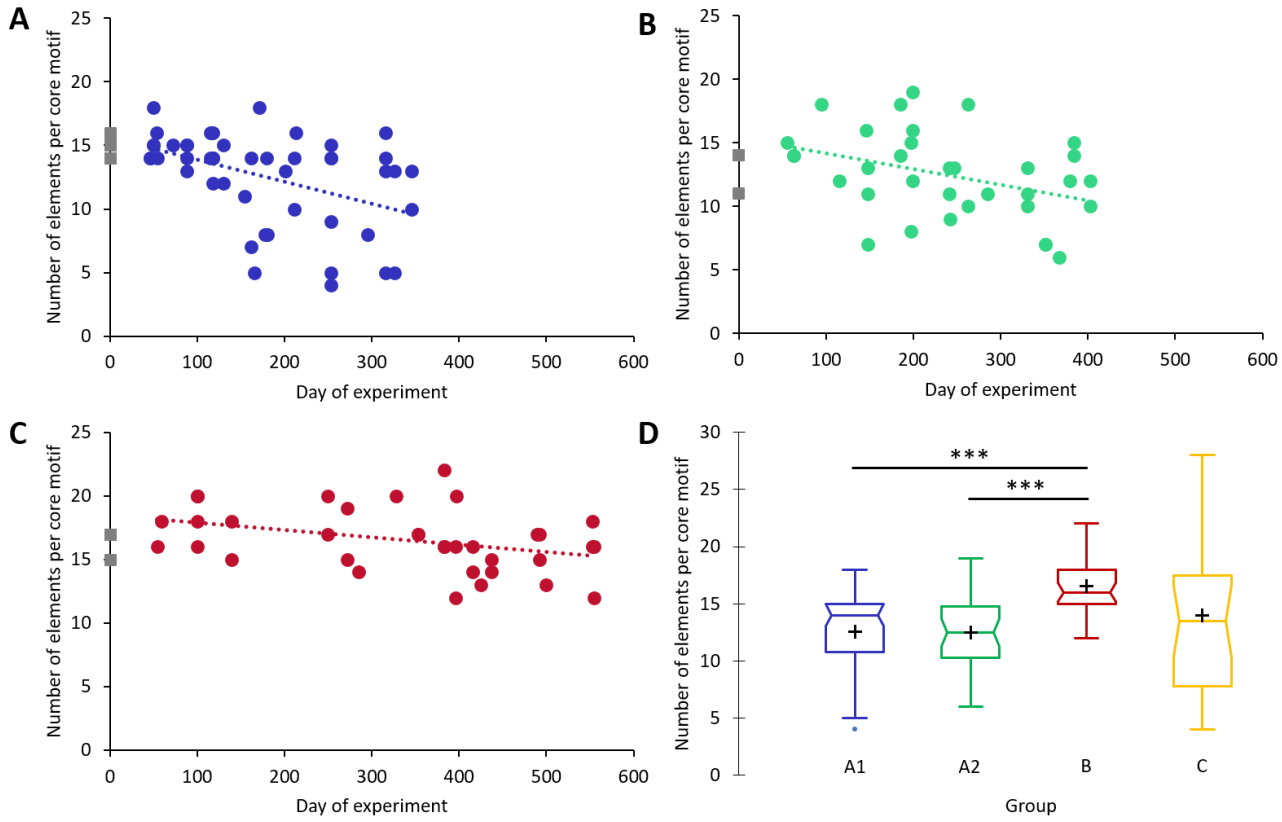

Figure 4. Simplification of the core motif structure over time in the three colonies

The number of elements per core motif significantly decreased over time in (A) colony A1 (r_s = -0.484, p < 0.001); (B) in colony A2 (r = -0.382, p = 0.026); and (C) in colony B (r_s = -0.429, p = 0.01).

In panel (A), (B) and (C), grey squares represent founder males. On the *x*-axis, each male is represented according to his hatching day in reference to the day of the experiment, day 0 of the experiment being the day when male founders were introduced into the aviary with naive females.

(D) Significant group differences in the number of elements per core motif (F = 27.9, df = 3, p < 0.001, see Table S5). Box-and-whisker plots depict the median, interquartile range and non-outlier range (whisker length up to 1.5 times the interquartile range). Crosses indicate mean values.

Additionally, there was a very high correlation between the number of elements per core motif and its duration (colony A1: $r_s = 0.849$, $p < 0.001$; colony A2: $r = 0.923$, $p < 0.001$; colony B: $r_s = 0.884$, $p < 0.001$). Accordingly, the results concerning the changes of core motif duration over time in our colonies were very similar to those concerning the number of elements per core motif: core motif duration slightly decreased over time but it was significant only in colony A1 and colony B (colony A1: $r_s = -0.414$, $p = 0.003$; colony A2: $r = -0.267$, $p = 0.126$; colony B: $r_s = -0.386$, $p = 0.022$, Figure S5).

Altogether, our results suggest that acoustic singularities can emerge and be maintained in colonies of zebra finches, even if the song core motif tends to simplify over time.

Groups differ in their use of the acoustic space according to their song model

We checked whether groups differed in the use of the acoustic space. Using the syllable parameters that were extracted on SAP 2011 for 300 syllables per male, we calculated Kullback-Leibler (K-L) distance to quantify song variability (Wu et al., 2008). The K-L distance is ideal to compare song repertoires in zebra finches, as it reduces the difficulty to identify resembling syllables in distinctive individual repertoires (Lansverk et al., 2019): the K-L method reduces the syllable sets of the two individuals being compared to two-dimensional scatter plots, compares the probability density function from the two sets and quantifies the difference (Wu et al., 2008). Therefore, the song variability assessed through the K-L distance provides a good proxy for the way birds differ in the use of the acoustic space. Each K-L distance is a score of the difference between two song repertoires. A good way of estimating group-level song variability is to measure the average K-L distance between all pairs of birds in this specific group. The song variability within each group is represented by the mean PC1 score obtained after running a principal component analysis (PCA) of K-L distances for each acoustic parameter (for more details, see STAR methods). Lower PC1 scores indicate that the

two repertoires being compared are similar, whereas higher PC1 scores indicate that the two sets of syllables have a lower similarity (i.e. songs are more dissimilar among the two compared individuals). We found a significant difference between groups in song variability ($\chi^2 = 266$; df = 3; $p < 0.001$; Figure 5).

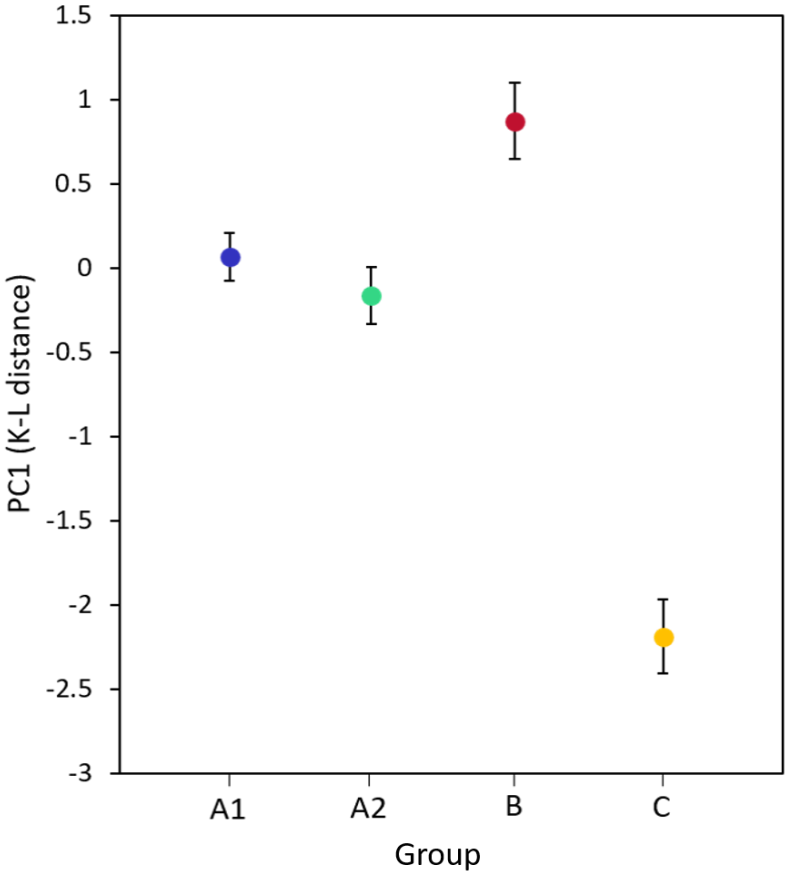

Figure 5. Song variability is higher when a song is imposed, and the use of acoustic space is determined by the song model

Fitted means and 95% confidence intervals of the principal component 1 (PC1) of population estimates of K-L in colony A1, A2, B and group C.

There was a significant difference in the PC1 scores of K-L between groups ($\chi^2 = 266$; df = 3; $p < 0.001$, see Table S3).

Among the four groups, colony A1 and A2 did not differ in their song variability but all the other groups did (Table S3). Colony B exhibited higher song diversity than the two colonies singing the song model A (Figure 5; Table S3). Song variability was significantly lower in

group C than in any of the three colonies (Figure 5; Table S3). These results suggest that because of their shared song model, colony A1 and A2 were using the same acoustic space, which led to the same observed song variability. Colony B having a different song model, males of this colony used a different acoustic space than birds of colony A1 and A2. This song model B allowed the birds to maintain a higher song variability in their colony. Colony C had a lower song variability than each of the other groups and we assume that the fact that different subjects were exposed to individually different song models is the cause of this result. To recall, birds of colonies A1, A2 and B were constrained to learn from males that were all singing an imitation of the same song motif. Thus, we can hypothesize that those birds would be inclined to introduce more variability around this core motif in order to be different from each other. This might lead to higher song variability. In conclusion, the lack of variability in the song model (core motif) imposed in the three colonies seems to be a major factor in determining the acoustic variability in a group of zebra finches. This acoustic variability is expressed at the syllabic level of song and can be used to differentiate the groups based on their early exposure to a single song model.

Towards artificial song dialects

So far, our results suggest that the four groups differed in the use of the acoustic space and that each song model determined a specific acoustic space. To check whether the three colonies represent three different song dialects, we conducted a Discriminant Function Analysis (DFA) based on the 13 song parameters of the core motif for each male of our four groups. This analysis led to a model accuracy of 89% (Table 1).

Table 1. Table of classifications resulting from the Discriminant Function Analysis (DFA) and leading to a model accuracy of 89%

Predicted \ Actual	A1	A2	B	C
A1	51	0	2	3
A2	0	34	0	5
B	3	0	36	1
C	2	0	0	15

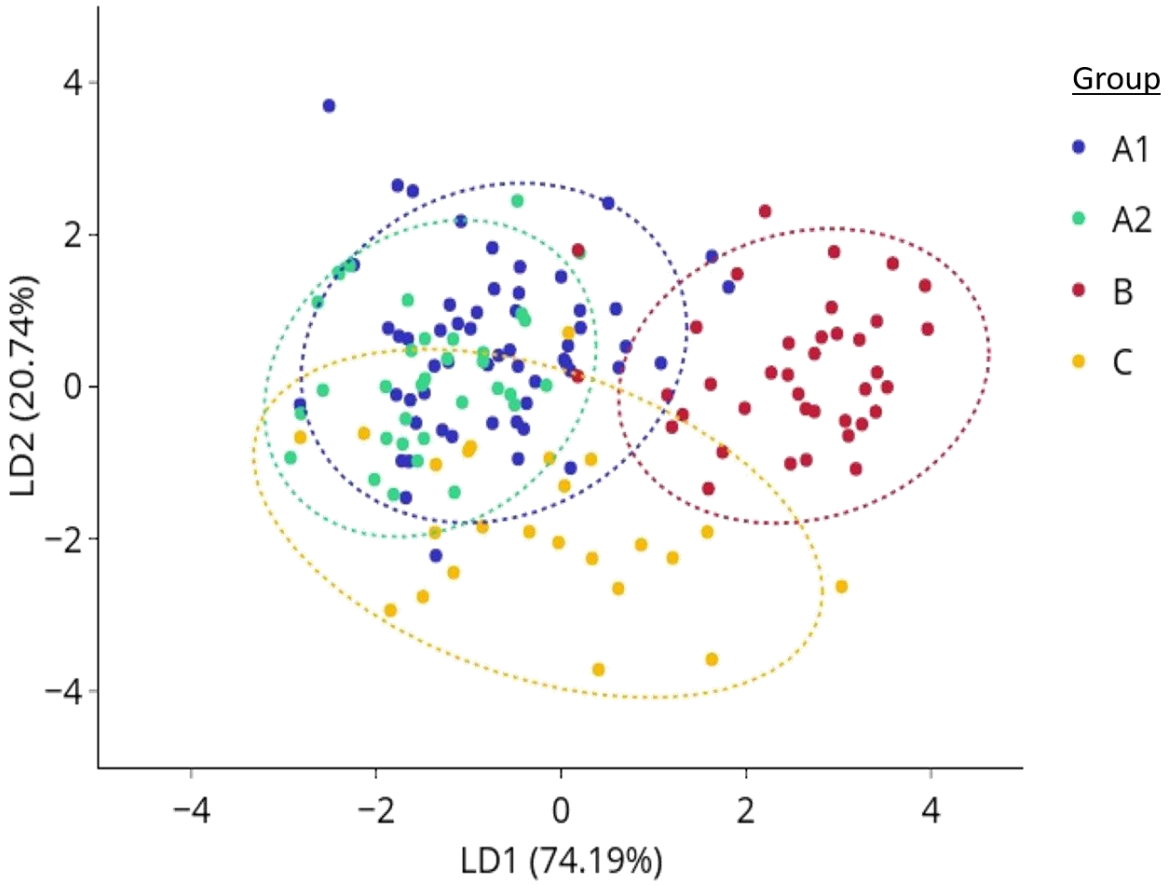

Figure 6. Artificial song dialects in the zebra finch

Results of the Discriminant Function Analysis (DFA): scatter plot of LD1 and LD2.

As shown in Figure 6, colony A1 and A2 overlapped with respect to the two discriminant functions (LD1 and LD2), colony B was separated from the two colonies singing the song model A and group C partially overlapped the three colonies. Once again, these results suggest

that the selection of founders singing a same song model in our colonies led to acoustic specificities within the core motif that permits to distinguish with high accuracy the origin of the birds.

Group differences in the song bout structure

In order to check whether these acoustic specificities at the motif level are linked to other levels of song bout organization, we looked first at the song bout structure. There was a significant difference between groups in the mean number of connector types per song bout ($F(3,67.1) = 14$, $p < 0.001$; Figure 2D). Colony A1 and A2 did not differ in terms of mean number of connector types produced per song bout. However, this number differed from colony B, as it was significantly higher in colony A1 and A2 than in colony B. Finally, colony A2 differed from group C, whereas colony A1 and B did not (Figure 2D; Table S4). This suggests that the two colonies singing the same song motif were closer to each other in terms of song bout structure than to the other two groups. By comparing mean scores of linearity, consistency and stereotypy per male (other metrics of song bout structure), we found no significant differences between any of our four groups (linearity: $\chi^2 = 4.93$; df = 3; $p = 0.177$; consistency: $\chi^2 = 3.49$; df = 3; $p = 0.322$; stereotypy: $\chi^2 = 4.53$; df = 3; $p = 0.210$).

Inter-syllabic gap duration as a proxy to characterise the temporal pattern of song bouts

We examined the distribution of inter-syllabic gaps in the four groups, a species-typical feature that represents the temporal patterning of song in zebra finches and that has been shown to be modulated independently from song syllable morphology (acoustic specificities of syllables; Araki et al., 2016; Tchernichovski & Lipkind, 2016). Empirical Cumulative Distribution Function (ECDF) of each group was calculated for the duration of all inter-syllabic gaps between the 300 syllables per male. Then, differences between groups were quantified

using Kolmogorov-Smirnov (KS) tests. The distribution of inter-syllabic gaps of colony A1 was more like the one of colony A2 than the one of colony B (Figure 7A), whereas cumulative distribution of group C inter-syllabic durations followed the ones of colony A1 and A2.

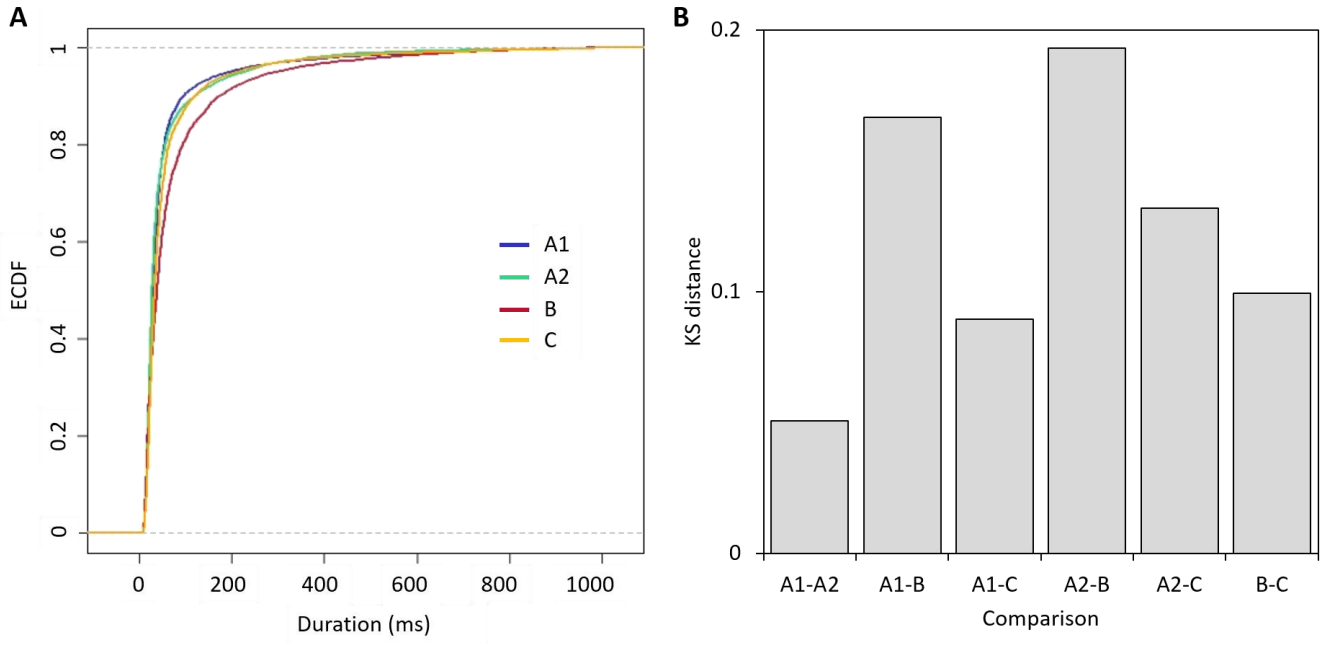

Figure 7. Colonies with a same song model are closer to each other in terms of inter-syllabic gap distributions

(A) The distribution of inter-syllabic gaps of colony A1 (blue line) is more similar to colony A2 (green line) than to colony B (red line). Cumulative distribution of group C inter-syllabic durations follows the ones of colony A1 and A2.

(B) KS distance for inter-syllabic gap durations for the six possible comparisons between A1, A2, B and C. The lowest KS distance is found between colony A1 and A2 and the highest between colonies singing the song model A and colony B.

Figure 7B shows the KS distances for inter-syllabic gaps duration for all six comparisons. Colonies A1 and A2 exhibited the lowest distance and the highest distances were found between colony B and the two colonies singing the song model A. Colonies' distances to group C were found in-between and differed according to the colony. These results showed that the two colonies singing the same song model exhibited the same distribution of their inter-syllabic intervals compared to the other groups.

Group differences at the syllabic and sub-syllabic level

At the syllabic level, we found no significant difference in the mean syllable duration (χ^2 = 4.43, df = 3, p = 0.218; Figure S3D). At the sub-syllabic level, we found a significant difference in the number of elements per core motif (χ^2 = 27.9, df = 3, p < 0.001; Figure 4D). Colony A1 and A2 were not different in the number of elements per core motif. However, this number was significantly lower in colony A1 and A2 than in colony B. Finally, no colony differed from group C (Figure 4D; Table S5). As for song bout structure, this again suggests that the two colonies singing the same song motif were closer to each other in terms of sub-syllabic organisation than to the other two groups.

The influence of social interactions in an artificial situation of song learning

In the zebra finch, the dynamics of the song learning process depends on the social interactions of juveniles with conspecifics, males and females, young and adults (Derégnaucourt, 2011). The choice of the song tutor by youngsters could be influence by several factors, such as the amount of parental care and interactions with the young (Williams, 1990), and the level of aggressiveness towards the young (Clayton, 1987; Jones & Slater, 1996). Most studies focus on the interaction with adults. However, there is also evidence that social interactions with peers can influence song learning (Derégnaucourt & Gahr, 2013; Tchernichovski & Nottebohm, 1998), and that a sibling may be as salient as an adult for a juvenile when evaluating potential song models (Derégnaucourt & Gahr, 2013). Finally, it has recently been discovered that an adult female's social feedback could also guide the process of song learning in young male zebra finches (Carouso-Peck & Goldstein, 2019).

In two colonies (A2 and B), we performed weekly observations of young males (colony A2, n = 29 males; colony B, n = 36 males) from dph 25 to dph 65. During these observations,

we noted all social interactions such as allopreening, clumping, pecking, etc. (see STAR Methods). Overall, we analysed 6410 dyadic interactions (colony A2: n = 2672; colony B: n = 3738). As expected, in both colonies, the later the focal subject hatched in the experiment, the more he had colony members to interact with (colony A2: $r = 0.715$, $p < 0.001$; colony B: $r_s = 0.823$, $p < 0.001$). We observed that 33.7% (in colony A2) and 25.8% (in colony B) of interactions concerned an older male (at least 30 days older), 22.4% (in colony A2) and 27.9% (in colony B) of interactions concerned an older female, 25.7% (in colony A2) and 22.8% (in colony B) of interactions concerned a young male (peer or younger) and 18.2% (in colony A2) and 23.5% (in colony B) of interactions concerned a young female (peer or younger). In colony B, there was no significant difference in the mean proportion of interactions between these four different conspecific categories ($\chi^2 = 3.79$, df = 3, $p = 0.285$). However, in colony A2 there was a significant difference between these categories ($\chi^2 = 17.9$, df = 3, $p < 0.001$): pupils interacted more with older males (Figure S6 & Table S6). Yet, pupils that interacted more with older males did not have a higher similarity score to the model than the other pupils ($F(2,26) = 0.973$, $p = 0.391$). On average, pupils of both colonies had more affiliative than agonistic interactions (colony A2: V = 337, $p = 0.009$; colony B: t = 5.13, df = 35, $p < 0.001$). Yet, the similarity score to the song model did not differ between males that had more affiliative interactions and males that had more agonistic ones (colony A2: W = 59.5, $p = 0.386$; colony B: t = -0.795, df = 29, $p = 0.433$). There was a positive significant correlation between the proportion of interactions with a male and the similarity score to the song model in colony B ($r_s = 0.409$, $p = 0.022$), but not in colony A2 ($r_s = -0.103$, $p = 0.596$).

For each pupil of the two colonies, we identified his major interactor (MI). In colony A2, most pupils had a male MI (78.9%) instead of a female (24.1%), whereas in colony B, 58.4% of pupils had a female MI and 41.6% a male. However, pupils that had males as a MI did not have a higher similarity score to the song model than pupils that had a female MI (colony

A2: t = 0.491, df = 27, p = 0.627; colony B: $t_{(w)}$ = -0.483, df = 28.6, p = 0.632). Additionally, we found no effect of the MI's sex on the nature (agonistic or affiliative) of social interactions (colony A2: W = 56, p = 0.294; colony B: W = 144, p = 0.676). In both colonies, more pupils had a peer or younger bird as a MI (colony A2: 72%; colony B: 78%), than an older MI. There was a significant effect of the MI's status, with older MIs being more aggressive to focal subject than peer or younger MIs (colony A2: $t_{(w)}$ = 6.69, df = 8.53, p < 0.001; colony B: W = 173, p = 0.021).

We then focused our analysis on interactions with males that could potentially have served as a song tutor. We removed female interactors from our data and identified the major male interactor for each pupil. For each pupil, we calculated his similarity score to his MI. When considering only interactions with male MIs, there was no significant correlation between song similarity and the age difference to the MI (colony A2: r_s = -0.072, p = 0.712; colony B: r_s = 0.085, p = 0.648) or the number of interactions with the MI (colony A2: r_s = 0.127, p = 0.512; colony B: r_s = 0.203, p = 0.273). We noticed that in both colonies, more pupils had a peer or a younger bird as a male MI rather than an older male MI (colony A2: 62%; colony B: 71%) and that the status of the male MI had an effect on the nature of social interaction, with older male MIs being more aggressive towards the focal subjects than peer/younger male MIs (colony A2: W = 19, p < 0.001; colony B: $t_{(w)}$ = 2.60, df = 9.46, p = 0.028). However, none of these factors had an effect on the song similarity score to the male MI: neither the age status of the male MI (colony A2: t = -0.349, df = 27, p = 0.730; colony B: t = -0.887, df = 29, p = 0.383), nor the nature of interactions with the male MI (colony A2: t = 1.27, df = 24, p = 0.215; colony B: t = -0.3, df = 28, p = 0.767).

The behavioural observations' results show that during their sensitive phase of song learning, birds affiliated with conspecifics of both sexes and of different age classes and not

preferentially with males (adult or young), and suggest that the degree or nature of interactions with males did not indicate how well the pupils learned their song.

CONCLUSIONS

Altogether, we demonstrated that artificial song dialects can be experimentally induced in zebra finches. Indeed, we found that the two colonies that had founder males singing the same song model shared the same acoustic specificities but differed from the colony with a different song model. This pattern was seen on all different levels of the zebra finch song: from the constitutive elements of the core motif to the song bout structure.

When focusing on song similarity to the model at the core motif level, our results suggest that offspring of the three colonies generally succeeded to maintain a faithful imitation of the song model, even late-hatched pupils. This demonstrates a certain conformity at the core motif level. Nevertheless, several changes over time in the three colonies such as a slight decrease of the similarity score over time in the colonies, a reduction of the number of elements within the core motif, a decrease of the core motif duration and a reduction of produced element clusters, show that the core motif simplified over time in the three colonies. Similarly, studies on cultural evolution of artificial languages in humans and pattern learning in primates suggest that a culturally transmitted behaviour will evolve in order to maximize its own transmission by becoming increasingly structured and easier to learn (Claidière et al., 2014; Kirby et al., 2008). Perhaps a similar process was at work in the current experiment.

Our results are also a strong invitation to take into account the macrostructural level of organization of the zebra finch song, namely the song bout structure. Indeed, we discovered that even if birds conformed to the song model at the core motif level, they integrated variability in their song bouts. In the three colonies, birds varied in the number of connector types they

used in song bouts, demonstrating a high inter-individual variability in the song bout structure. This highlights the fact that birds were able to innovate within their song bouts by producing a variety of connectors, and thus diverge from the original song model. However, this diversification at the song bout level did not imply that song bouts would be less stereotyped over time, since we found no evidence for changes of linearity, consistency or stereotypy over the course of the experiment in the three colonies. The fact that inter-individual variability in the song bout appeared in the three colonies indicates that this phenomenon was not inherent to the type of song model. In addition, it is likely that this was also not due to the pre-existing variability in the song bout structure of the founder males since the results were similar in the three colonies whatever the number of male founders or the song model.

At the syllabic level of song, syllable duration did not significantly decrease over time in two of the three colonies, whereas core motif duration did. That implies that the simplification process only concerned the constitutive unit of the song, corresponding to the colony's song model, and that it did not impact uniformly all syllables that could be produced in the song. This way, individuals managed to maintain an overall complexity in the rest of the song surrounding the core motif. Together with the observed high inter-individual variability in the number of connectors per song bout, these findings revealed a major individual variation in the song bout structure, leading to a global song diversity at the colony level.

Those rapid changes and variability in song bout structure could emerge from innovations or copy errors and may facilitate individual recognition and thus coordination between individuals during vocal interactions. On one hand, using an operant discrimination task (go no-go procedure), it has been demonstrated that song bout structure was the less salient acoustic feature in guiding individual vocal recognition in zebra finches, when local fine structure of syllables and song bout structure provided conflicting information (i.e. local fine

structure indicating the identity of one singer whereas song bout structure indicating the identity of another singer) (Geberzahn & Derégnaucourt, in preparation). But on the other hand, it has been demonstrated that individuals capable of vocal flexibility can potentially use it to express different behavioural states through their songs (Hyland Bruno & Tchernichovski, 2017). Additionally, in natural conditions the song of a zebra finch constitutes an individual signature (Clayton, 1988; Cynx & Nottebohm, 1992). Even if all males sing the same song type, zebra finches are capable of individual vocal recognition (Geberzahn & Derégnaucourt, in preparation). Nevertheless, a song divergence from the original song model could help reinforcing individual signature and play a role in improving vocal recognition between birds.

Taken together, our results are the first experimental demonstration that cultural evolution can shape oscine birdsong at different scales of the song structure. Our predictions that we would find either a high conformity in the song leading to a stable dialect, or a high amount of inter-individual variability preventing the establishment of song dialects and leading to an unstable drifting culture, were both not completely confirmed. We rather found that conformity and variability were not exclusive, and could each be expressed in different parts of the song in a complementary way, without preventing the emergence and stability of song dialects in artificial conditions.

Despite what was suggested in another study (Lachlan et al., 2016), zebra finches can elaborate and maintain song dialects in a specific context of laboratory-controlled experiments. This suggests that even though learning errors could favour within-population variability, it was not a sufficient diverging force to prevent the establishment of artificial dialects. Instead, imitation and innovation (or copy errors) – two opposed social forces that can shape cultures – appear to be complementary and act together in shaping these artificial song dialects. Therefore, our results follow the balanced mechanism proposed by Tchernichovski and collaborators

(2017) that lead to stable polymorphic cultures such as birdsong dialects. In this context, we can say that the artificial song dialects we created can be considered as polymorphic vocal cultures. However, it should be noted that in those laboratory conditions, zebra finches could not migrate to or exchange with other groups. In the field, as suggested by Zann (1993), nomadic behaviours of natural populations prevent the establishment of song dialects in the zebra finch. Additionally, we could not assess the stability of the artificial dialect we created, since we only followed them for approximately 500 days. In this context, it is difficult to evaluate whether such dialects will remain stable over longer periods of time. Nevertheless, it has been demonstrated that a conformist bias associated with a moderately precise song learning would allow bird vocal cultures to match the stability of human cultures (Lachlan et al., 2018). Indeed, in swamp sparrows (*Melospiza georgiana*), syllable types could persist for more than 500 years (Lachlan et al., 2018). In our case, a similar situation could arise if, as we demonstrated, most birds would continue to conform to the song model.

As mentioned before, different aspects of social interactions during the sensitive phase can shape song learning in zebra finches, such as the amount of interactions (Williams, 1990), the nature of interactions (Clayton, 1987; Jones & Slater, 1996), the age of the interactor (Derégnaucourt & Gahr, 2013; Tchernichovski & Nottebohm, 1998) or its sex (Carouso-Peck & Goldstein, 2019). However, in our study we could not identify any clear pattern between any of those factors and the ability to produce a good imitation of the song model in the observed birds of the two colonies. Instead, our behavioural observations suggest that song learning in zebra finches is not an acoustic phenomenon per se but involves multimodal signals shaped by social interactions with individuals that are not necessarily adult males (Derégnaucourt & Gahr, 2013; Carouso-Peck & Goldstein, 2019). Because in our study, a lot of youngsters interacted with females as much as with males and even had a female as major interactor, it is very likely

that both males' and females' feedbacks influenced song learning in our colonies, and thus, the establishment of the artificial dialects.

Beyond social aspects, birdsong learning also depends on a genetically determined circuitry that interacts with experience (Haesler et al., 2007; Liu et al., 2015; Mets & Brainard, 2017). Therefore, the observed individual differences in song could depend on genetic mutations at the individual level and drive vocal changes at the population level. Such mutations could also explain why some birds did not provide a good copy of the original song model.

In songbirds, dialects can play a role in sexual selection, with females preferring to pair with males singing the natal song dialect (Eastzer et al., 1985; King et al., 1980; Marler & Tamura, 1962; Searcy & Andersson, 1986). Additionally, it has been demonstrated that song dialects could signal group identity (Briefer et al., 2008; Hausberger et al., 2008) and could favour group cohesion (Hausberger et al., 2008). With the discovery that song dialects can be artificially created in laboratory conditions in the zebra finch, such aspects could be easily tested and would consolidate this species as a model of choice to study both proximate and ultimate aspects of vocal learning.

STAR METHODS

KEY RESOUCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software		
Avisoft SASLab Pro	Avisoft	https://www.avisoft.com/
GoldWave 6.31	GoldWave	https://www.goldwave.com/
Jamovi 1.0.7	Jamovi	https://www.jamovi.org/
Sound Analysis Pro 2011	Tchernichovski et al., 2000	http://soundanalysispro.com/
Sound Explorer	René F. Jansen, University of Amsterdam	https://github.com/ornith/SoundExplorer_Stuff
SongSeq 1.1	Daou et al., 2012	https://www.math.fsu.edu/~bertram/software/birdsong/JNM_12/
R 3.5.1	R Development Core Team	https://www.r-project.org/

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Lucille Le Maguer (lucille.lemaguer@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Subject Rearing and Housing

To create the colonies, we used 16 adult males and 16 females hatched and raised at the University Paris Nanterre (France) or the Max Planck Institute for Ornithology (MPIO) in Seewiesen (Germany). Females were raised by both parents until dph (day post hatch) 14, and then by their mother alone to avoid any imprinting on male song. For the first colony, we used adult males (n = 10) that were raised at the MPIO and that were selected according to their song structure (see below). In addition, we used recordings of songs from 24 adult males from the general pool of the MPIO. Those birds were raised freely in communal aviaries in which males sang different songs, without any attempt to control for birdsong learning.

For the three colonies, we placed founder males with founder females in large flight aviaries (3.18 x 3.32 x 2.84 m) where they could pair and breed freely. We equipped aviaries with plastic nest boxes, and we provided birds with coconut fibers and cotton nesting material. Nest boxes were controlled daily, and we individually marked each nestling with one numbered and two coloured leg bands for identification. In aviaries, birds were provided with water, seeds mix and egg food for exotic finches, sand and cuttlebones *ad libitum*. Once a week they received supplemental vegetables and fruits. Once a month, they were given hard-boiled eggs. All aviaries were maintained between 20 and 23°C and set to a 14:10 light:dark (LD) schedule. The three colonies were kept in three different aviaries, visually and acoustically isolated from each other so that the birds could not hear another type of song than imitations of the song model that had been used to train the founders. Founder males of those three colonies were selected from a larger pool of birds that were trained to produce a same copy of a song model using different methods (see below and Table S7). The day we introduced males and females into the aviary is considered the day 0 of the experiment. Two founder males died before the first pupil had hatched, leaving us with eight founder males. Breeding went on until we obtained at least 30 male pupils in each colony. This lasted 346 days in colony A1 to obtain 50 males, 402 days in colony A2 to obtain 34 males and 555 days for colony B to obtain 38 males. During reproduction, each nest box was checked every day to verify the number of eggs, the hatching day of pupils and the potential social parents.

Colony A1

For this first colony, we selected ten founder males hatched and raised in the MPIO and they were trained using different methods (see Table S7). Some males were trained in sound proof chambers. Those males had previously been raised in separate breeding cages (LD 12:12) by both parents until dph 10 when the mother and young were transferred to another room

without any adult male to avoid imprinting on males' song. At dph 35, each young male was isolated in an individual sound proof chamber (LD 12:12). After a week of isolation (dph 43), each young bird was exposed to the song model A (Figure 1A) using an operant conditioning procedure until dph 100 (Adret, 1993a, 1993b; Derégnaucourt et al., 2013). Usually this procedure results in some interindividual variability: some males produce a good copy while others produce a bad copy. The quality of copying was measured using a semi-automatic procedure (see below). Some males that produced a good copy were used as live tutors in a one-to-one tutoring procedure (see Derégnaucourt et al., 2013): young males were raised as explained above and when they reached 43 dph, they were exposed continuously to a live tutor until dph 100. This procedure usually results in a high song copying accuracy (Derégnaucourt et al., 2013).

Before our experiment started, the song of the ten founder males of colony A1 were recorded in sound proof chambers (see below in the "song recordings" section) and those that produced a close copy to song model A were selected as founders of the colony. From the original pool of birds, six males out of ten were trained in sound proof chambers: four with an operant conditioning technique and two with one-to-one live tutoring (Table S7). The remaining four hatched in the aviary in which we kept males producing a good copy of song model A with females raised in acoustic isolation from males until adulthood (Table S7).

Colony A2

Colony A2 was founded by three males hatched in colony A1. A few months after their song has crystallised, song of founder males of colony A2 were recorded in sound proof chambers (for details see below in the "song recordings" section). Founder males were selected based on the quality of imitation of the song model A.

Colony B

All three founder males of colony B were trained with operant conditioning to reproduce the song model B (Figure 1A), using the same method as described before for colony A1. A few months after the end of training, the song of founder males of colony B was recorded in sound proof chambers (see below in the “song recordings” section).

Summary

Table S7 gives a summary of the numbers and training method for male founders of the three colonies. The colonies' song models we refer to in our experiment - song model A for colony A1 and A2, and song model B for colony B (see Figure 1A) - correspond to the songs used for operant training. These song models were not artificial but produced by adult birds.

Ethical Note

The study complies with the European regulations regarding animal experimentation. Experimental authorization was provided by the French Ministry for National Education, Higher Education and Research (authorization no. 02609.02).

METHOD DETAILS

Song recordings

All founder males were recorded at least twice: once a few months after training (for selection) and once after breeding in the colony was terminated, when all males of the colony (founders and pupils) where recorded for analysis. Males hatched in the colonies were recorded in sound proof chambers once the last male hatched in the colony was at least 100 days old: for colony A1 recordings were carried out at dph 173 (± 58); for colony A2 they were carried out at dph 296 (± 149), and for colony B they were carried out at dph 314 (± 143). For song

recordings, all males where individually placed in a sound proof chamber. Sound proof chambers (85 x 65 x 60 cm) were equipped with fans providing a low airflow in the chamber and OSRAM DULUX lights on an automatic 14:10 light:dark schedule. Within sound proof chambers, males were housed in cages (46 x 22 x 26 cm) and provided with water, food, sand and cuttle bones *ad libitum*. Each cage was equipped with two mirrors (10 cm diameter), one on each perch, to reduce the impact of social isolation. We recorded each male's vocal activity continuously using SAP 2011 (Sound Analysis Pro software; Tchernichovski et al., 2000) ran by a DELL Optilex GX620 PC on Windows 7. During continuous recording, SAP detects and saves individual song bouts into separate files, whilst mostly discarding isolated calls and cage noises. We used a PreSonus AudioBox (24 bit/96K) recording interface connected to a Behringer C-2 microphone placed above the cage.

Song analysis

As mentioned earlier, two founder males of colony A1 died before the hatching of the first young. They were excluded from the analysis. The total number of males kept for analysis were: 56 birds (8 founders, 48 pupils) for colony A1; 37 birds (3 founders, 34 pupils) for colony A2 and 38 birds (3 founders, 35 pupils) in colony B. The analysis also included a group of birds from the general pool at the MPIO (group C) that was composed of 24 birds.

We used a standardized procedure of song selection and analysis for all the males of the four groups (three colonies and group C). For each male, we selected the first thirty files containing song in the morning of the last day of recording. Using the Goldwave software (v6.36), we applied a highpass filter at 420 Hz (Lachlan et al., 2016) and a volume maximization of 90% to all the 30 sound files for each male. For our analysis, we segmented the song into different units using SAP 2011 (see below). For each segmented unit of the song, SAP 2011 extracted 14 different parameters from the sound: duration, amplitude, pitch, frequency

modulation (FM), squared amplitude modulation (AM^2), Wiener entropy, goodness of pitch, mean frequency and the variance in pitch, FM, entropy, pitch goodness, mean frequency and AM (see SAP 2011 manual: http://soundanalysispro.com/manual-1). However, for most of the following analyses, we only kept 13 of these parameters, by excluding amplitude (see below).

Analysis based on the core motif

By comparing the song of each male (founders and offspring) to the song model of his colony, we were able to identify the "core motif" (Figure S1). The core motif of a bird is the closest repeated song unit to the song model of his colony. Depending on the male, the core motif is either identical to the motif, or different. The motif is the largest repeated unit of the song. In some males, the motif is larger than the core motif because additional syllables adjacent to the core motif are integrated in the motif. After visually inspecting spectrograms of all the 30 song files for each male, we were able to identify the main core motif and sometimes one or two additional versions of the core motif produced by a male. We refer to the most abundant core motif of a male as his "core motif #1". "Core motif #2" and "core motif #3" were less abundant versions of his core motif. After identifying the different versions of core motifs in the song of each male, we selected one song file for each bird and for each version of core motif. We then delimitated the beginning and the end of one core motif of each version per male using SAP 2011. As the term "core motif" defines a song unit identified based on the uniform song model of a given colony, we did not determine core motifs for birds of group C: because those birds all had learned their song from a different song model, there was no core motif. Thus, for these birds we identified only the motif.

Similarity score

We prepared one sound file per version of core motif for each male by cutting the sound at the onset and offset of the core motif, using Avisoft SASLab Pro. To quantify how well founders and pupils the core motif of the colony's song model, we used the similarity module of SAP 2011 (Tchernichovski et al., 2000). Similarity scores generated with this procedure are calculated as percentages of similarity and reflect the amount of the song model's sounds included in the pupils' motif. They are calculated on long intervals (usually 50-70 ms). Each core motif from each subject was compared to that of the colony's song model. When focusing on the changes of the song model's imitation over time in the three colonies, we kept only the highest similarity score to the song model for males who produced more than one type of core motif.

Element analysis

In the song motif, vocal changes such as abrupt changes in amplitude or entropy permit to delimit vocal gestures (Amador et al., 2013; Lachlan et al., 2016). In SAP, we identified delimitations of such changes in the core motif (called "time events"), using amplitude and entropy thresholds (Figure S7). We identified and annotated time events for each type of core motif of each male. Syllables are independent song units characterized by the presence of a silent gap between them. Syllables of core motifs were segmented into fine-grained units referred to as "elements" (Figure S1 & S7). Time events thus delimitate the onset and offset of elements. To analyse each element in the core motif, we segmented them manually based on time events using SAP 2011. This allowed us to extract 13 acoustic parameters (previously mentioned) per element.

When investigating the changes of the number of elements per core motif over time in the three colonies, we based the analysis solely on core motif #1 of each male (the most frequently produced motif), as not all males produced more than one version of the core motif.

Because in control group C males did not have a unique song model, we could not identify a core motif. Therefore, we segmented elements of the classical motif. In this article, when referring to the core motif, one should keep in mind that for group C the core motif was equivalent to the motif.

Discriminant Function Analysis (DFA)

To examine whether core motifs from our different groups can be distinguished by their acoustic properties, we conducted a Discriminant Function Analysis (DFA) by taking into account the 13 song parameters of core motif #1 for each male of our four groups. The DFA constructs new parameters so-called "discriminant functions" (DF) in such a way that the separation of groups along the axes is maximized. Each DF contributes more or less to the groups' separation.

Analysis based on the entire song

Syllable segmentation for further analysis

For each male of the three colonies, we segmented songs into syllables using SAP. This allowed us to visually inspect all syllables and to select only those without cage noise. For each male, we segmented a minimum of 300 syllables. For 6 males we could not obtain enough song material, subsequent analyses were therefore based on 193 ± 53 syllables for those males. In total, 48,406 syllables were segmented for which 14 acoustic parameters were measured (see above). Results were loaded into the SongSeq software (Daou et al., 2012). This allowed us to obtain different syllable clusters for each male, each cluster representing one type of syllable

produced by the male. Excel files generated by SongSeq were then further processed using a custom-made program written in MATLAB (R2017a Update 3) in order to cut larger sound files into one wav file per syllable. We created a folder for each cluster, containing the corresponding wav files. We checked that this clustering was appropriately done by visually inspecting spectrograms and listening to sounds, using Sound Explorer (René Jansen, University of Amsterdam) and Avisoft SASLab Pro. If needed, syllables were re-assigned to the appropriate cluster.

Song bout analysis

Typically, zebra finch song is produced in *bouts*; each bout is formed by introductory syllables, followed by one or several motifs, sometimes separated by other syllables (Hyland Bruno & Tchernichovski, 2017). Those syllables are called "connectors" and are often call-like sounds or amplified introductory syllables (Hyland Bruno & Tchernichovski, 2017). Each song bout can be defined as a period of uninterrupted singing with only short silent gaps. To be able to analyze the song bout structure in a standardized way for all birds in a specific group, we determined one bout criteria per colony using a log survivor function (Sibly et al., 1990; Slater & Lester, 1982). In colony A1 and A2, two song bouts were separated by a minimum silence of 200 ms. In colony B and group C, the bout criterion was 250 ms. For some males it was obvious after visual inspection of spectrograms that the first criterion was not appropriate. In this case, the criterion was adapted.

For bout analysis we ran a MATLAB custom-made program using the pre-defined bout separation criterion. This analysis provided for each song bout the total number of syllables, the number of different syllable types, the number of different transitions, the bout duration and three different scores used to assess song stereotypy: the linearity, consistency and stereotypy score (Scharff & Nottebohm, 1991). The linearity score represents how often syllables are sung

in a specific order. In our study we calculated a slightly modified linearity score, as follows: linearity = (number of different syllables – 1) / number of syllable-to-syllable transitions (Iyengar & Bottjer, 2002; Kao & Brainard, 2006; Zevin et al., 2004). The consistency score represents how often specific variations of the song bout occur. In other words, it does not represent how syllables are ordered but the amount of time a particular sequence of syllables is sung. It was calculated following the equation: Consistency = $\sum$ [T(d)/T(a)]/N; where T(d) is the most frequent/dominant transition for each syllable, T(a) is the number of all transitions for that particular syllable and N is the total number of syllable types in the song (Scharff & Nottebohm, 1991; Iyengar & Bottjer, 2002; Zevin et al., 2004). The overall stereotypy in the song is represented by the stereotypy score, which is the mean of linearity and consistency scores: Stereotypy = (linearity + consistency)/2. All scores were calculated for each song bout (including introductory syllables) of each male of the four groups.

Kullback-Leibler (K-L) analysis

We estimated Kullback-Leibler (K-L) distances to quantify song variability. We used the method described in Wu et al. (2008) to obtain the K-L distances. K-L distances were calculated for 12 out of 13 song parameters obtained in SAP 2011 after manual song segmentation of 300 syllables per males, syllable duration (the 13th parameter) being used in each K-L distance calculation. Each K-L distance is a score of the difference between two song repertoires. A good way of estimating group-level song variability is to measure the average K-L distance between all pairs of birds in this specific group. One matrix of pairwise comparisons was generated for each of our four groups. In this full K-L matrix, one individual bird was used twice in each pairwise comparison: once as a “target” and once as a “template”. The resulting two values per pair of birds were averaged to obtain so-called “estimates” (cf. Lansverk et al., 2019).

K-L distances based on each song parameter were highly correlated, as measures of K-L all represent song dissimilarity. Thus, we conducted a principal component analysis (PCA), on K-L distance estimates for each of the 12 acoustic parameters (see "Quantification and Statistical analysis" section below).

Analysis of inter-syllabic gaps

To assess the distribution of inter-syllabic gaps in the four groups, we calculated all inter-syllabic gap durations between the 300 syllables for each male. After excluding the few males for which we had not a minimum of 300 syllables, we found a minimum number of 216 inter-syllabic gaps. Thus, we selected the first 216 inter-syllabic gaps for each male of the four groups. When examining the distribution of these inter-syllabic gaps, we found a plateau beneath 10 ms and over 1000 ms. For the analysis, we kept only the inter-syllabic gaps with a duration between 10 and 1000 ms. We compared the distribution of inter-syllabic gaps in each group by plotting their Empirical Cumulative Distribution Functions (ECDFs). Differences between groups were quantified using Kolmogorov-Smirnov (KS) test.

Cluster analysis

Cluster analysis on syllables was performed using the 13 acoustic parameters that were extracted from 300 syllables per male. Founder males were included in this analysis. Cluster analysis on elements was performed using the 13 acoustic parameters that were extracted from the segmentation of elements in each male's core motif. If a male produced several versions of the core motif, elements from each of his core motifs were taken into account in the analysis. As in Lachlan et al. (2016), we used a clustering method based on Bayesian Gaussian Mixture models (BGM), with the Mclust package and function in R (Fraley & Raftery, 2006). Default parameters of this function being set at G = 9 (defining a maximum of 9 clusters), we first found

a total of 9 clusters in our analysis. To find the appropriate G setting, we performed a clustering analysis using a G of 9 (default), 10, 20, 30, etc., until we did not reach the same maximum number of clusters anymore. Using a G = 30 for syllable clustering, the optimal syllable clustering model (type VVV) found evidence for 26 clusters. While for the element clustering, using a G = 20, the optimal element clustering model (type VEV) found evidence for 15 clusters.

We noticed that colony A1 and A2 were close to each other in terms of cluster types repartition compared to the other two groups, especially for the repartition of the element cluster types (Figure 3C & 3D). To investigate the specificity of sound clusters to a song model rather than a colony, we summed the number of occurrences of each cluster between colony A1 and A2 to consider them as one and only group representing the song model A. This left us with three groups: group A, representing the song model A (colony A1 and colony A2), group B representing the song model B (colony B) and group C, not representing any uniform song model. Then, we only used percentages to investigate whether some clusters were specific to a song model.

Analysis of social behaviour

We conducted observations of social interactions of all pupils during the sensitive phase of song learning, from dph 25 to dph 65. In total, 29 males were observed in colony A2 and 36 in colony B. These observations consisted of a focal sampling of ten minutes of each pupil, three times a week. During the ten minutes of focal sampling, we noted all social interactions in which the bird was involved. The observer was hidden behind a curtain outside the aviary and used a Philips Voice Tracer to quietly describe all social interactions. These descriptions included the nature of the behaviour observed, for example clumping, allopreening, begging, courtship (affiliative behaviours); chasing, pecking, avoiding (agonistic behaviours) (see Table

S8: list of social behaviours; Elie et al., 2011; Zann, 1996). Descriptions of all behaviours were then coded to obtain one excel file for each day of observations.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were performed in R and Jamovi. All analyses were two-tailed, significance level was $p < 0.05$. All assumptions were checked before any statistical test. We used nonparametric tests where data were not normally distributed. For correlations, we used Pearson's product correlations for normally distributed data and Spearman's correlations if data were not normally distributed.

Following the cluster analysis (see "Cluster analysis" section above), we compared the occurrence frequencies of the different syllable and element clusters between the four groups. This was done with two different Pearson's Chi-Squared tests: one for syllables clusters and one for element clusters (Figure 3C & D).

We conducted a principal component analysis (PCA) on K-L distance estimates for each of the 12 different song parameters (cf. section "Kullback-Leibler (K-L) analysis") using the *PCA* function in R. This PCA included all the birds of our four groups. The output of our PCA showed that only one PC was significant, with an eigenvalue of 7.9, and explained 66% of the variation of the song data. The 12 song parameters had similar loadings on PC1, from 0.25 for the squared AM to 0.31 for variance in the FM. All song parameters being highly correlated with PC1, we chose to summarize K-L distances in the four groups by using PC1 as a measure of song variability and so, as the principal response variable in the statistical tests. Using the average of PC1 scores within each group, we tested for differences in song variability among the three colonies and the group C. This was done by running a Kruskal-Wallis H test (Figure

5). Dwass-Steel-Critchlow-Fligner pairwise post-hoc comparisons were then calculated between each group (Table S3).

We conducted a Discriminant Function Analysis (DFA) based on the 13 acoustic parameters of each male's core motif in the four groups (cf. section “song analysis”). This DFA was done using a linear discriminant analysis with the *lda* function in R. The percentage of separation achieved by the first discriminant function (LD1) was 74.19%, 20.74% by the second discriminant function (LD2) and 5.07% for the third (LD3). This indicated a good separation of groups by the first two LDs (Figure 6).

When testing for song differences between the four groups at the song bout structure, we examined the mean number of connector types produced per song bout. Group differences in this variable were assessed with a one-way ANOVA (Figure 2D). The Levene’s test for equality of variances was significant ($F(3,137) = 4.59$, $p = 0.004$), showing that the ratio of variances was not equal to 1. Therefore, we conducted a Welch’s ANOVA. Post-hoc comparisons were performed using a Games-Howell test for unequal variances (Table S4). We also examined group differences in the mean scores of linearity, consistency and stereotypy using three different Kruskal-Wallis tests (one per score). Group differences in the temporality of songs were assessed using the *ecdf* and *ks.test* functions in R on inter-syllabic gaps durations (Figure 7).

At the syllabic level, we compared mean syllable duration in each of the four groups using a Kruskal-Wallis H test (Figure S3D). At the sub-syllabic level, we used the same statistical test to check for group differences in the number of elements per core motif (Figure 4D). At the sub-syllabic level, post-hoc pairwise comparisons were conducted using Dwass-Steel-Critchlow-Fligner tests (Table S5).

Concerning the data on social interactions, we checked whether young males interacted more with a specific category of conspecifics when they were young. We tested differences in the mean proportion of interactions with each category of conspecifics within each colony, using a Friedman ANOVA for repeated measurements followed by post-hoc tests where appropriate: we used Wilcoxon signed rank tests for pairwise comparisons of each category of conspecifics (Table S6). To control whether pupils who interacted more with older males had a higher similarity score to the model in this colony, an ANOVA assuming equal variances (Fisher's ANOVA) was conducted after a non-significant Levene's test: $F(2,26) = 0.20$, $p = 0.82$. To verify whether pupils had more agonistic of affiliative interactions, we tested differences between the proportion of agonistic and affiliative interactions using a Wilcoxon signed rank test for colony A2, and a paired t-test in colony B. To check whether the similarity score to the song model differed between males that had more affiliative interactions and males that had more agonistic interactions, we attributed them to two different groups. Differences in similarity scores between two groups were assessed through a Wilcoxon rank sum test with continuity correction for colony A2, and a Student's t-test for colony B. Correlations between the proportion of interactions with a male and the similarity score to the song model were calculated using Spearman's correlations.

When considering only social interactions with the major interactor (MI) of each male offspring, we checked whether pupils that had a male MI had a higher similarity score to the model than pupils that had a female MI. We separated them in two groups and performed Student's t-test on similarity scores for colony A2. In colony B, we used a Welch's t-test because the assumption of equal variances was violated ($F(1,29) = 6.77$, $p = 0.014$). When searching for an effect of the MI's sex on the proportion of agonistic interactions with this MI, we used Mann-Whitney U-tests. We separated pupils in two groups according to the age status

of their MI (older or peer/younger) and also used a Mann-Whitney test on proportion of agonistic interactions with the MI in colony B, but a Welch's t-test in colony A2.

When considering only social interactions with the male MI, we split pupils into two categories: the ones with an older male MI and the ones with a peer or younger male MI. Differences in the proportion of agonistic interactions with the male MI between these two groups were assessed through a Mann-Whitney U test for colony A2, and a Welch's t-test for colony B. Finally, to see whether the age of the male MI, and/or the nature of most interactions with the MI influenced the similarity score to this MI, data was split up into two categories for each parameter of interest. When focusing on the age of the male MI, male offspring were classified either in the category of those having an older male MI, or the one of those having a peer or younger male MI. When focusing on the nature of most interactions with the male MI, pupils were classified in either one of the following categories: the ones which had more agonistic than affiliative interactions with their male MI, or the ones which had more affiliative than agonistic interactions with male MI. We tested for differences in the similarity score to the male MI between each of the two categories we created, using one Student's t-test for the categories concerning the age of the male MI, and another Student's t-test for the categories concerning the nature of most interactions with the male MI. This was done for each of the two colonies.

DATA AND SOFTWARE AVAILABILITY

All custom-made program written in MATLAB are available by contacting the first author, Lucille Le Maguer (lucille.lemaguer@gmail.com).

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AUTHOR CONTRIBUTIONS

S.D. designed the experiment with modifications by N.G. L.L.M, N.G., L.N. and S.D. performed research. L.L.M., N.G. and S.D. analysed the data. L.L.M, N.G., L.N. and S.D. wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

Adret, P. (1993a). Operant conditioning, song learning and imprinting to taped song in the zebra finch. *Animal Behaviour*, *46*(1), 149–159.

Adret, P. (1993b). Vocal learning induced with operant techniques: An overview. *Netherlands Journal of Zoology*, *43*, 125–125.

Amador, A., Perl, Y. S., Mindlin, G. B., & Margoliash, D. (2013). Elemental gesture dynamics are encoded by song premotor cortical neurons. *Nature*, *495*(7439), 59–64. https://doi.org/10.1038/nature11967

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*(7540), 538–541.

Araki, M., Bandi, M. M., & Yazaki-Sugiyama, Y. (2016). Mind the gap: Neural coding of species identity in birdsong prosody. *Science*, *354*(6317), 1282–1287. https://doi.org/10.1126/science.aah6799

Boncoraglio, G., & Saino, N. (2007). Habitat structure and the evolution of bird song: A meta-analysis of the evidence for the acoustic adaptation hypothesis. *Functional Ecology*, *21*(1), 134–142. https://doi.org/10.1111/j.1365-2435.2006.01207.x

Briefer, E., Aubin, T., Lehongre, K., & Rybak, F. (2008). How to identify dear enemies: The group signature in the complex song of the skylark *Alauda arvensis*. *Journal of Experimental Biology*, *211*(3), 317–326. https://doi.org/10.1242/jeb.013359

Brumm, H., Zollinger, S. A., Niemelä, P. T., & Sprau, P. (2017). Measurement artefacts lead to false positives in the study of birdsong in noise. *Methods in Ecology and Evolution*, *8*(11), 1617–1625. https://doi.org/10.1111/2041-210X.12766

Carouso-Peck, S., & Goldstein, M. H. (2019). Female Social Feedback Reveals Non-imitative Mechanisms of Vocal Learning in Zebra Finches. *Current Biology*. https://doi.org/10.1016/j.cub.2018.12.026

Claidière, N., Smith, K., Kirby, S., & Fagot, J. (2014). Cultural evolution of systematically structured behaviour in a non-human primate. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797), 20141541. https://doi.org/10.1098/rspb.2014.1541

Clayton, N. S. (1987). Song tutor choice in zebra finches. *Animal Behaviour*, *35*(3), 714–721. https://doi.org/10.1016/S0003-3472(87)80107-0

Clayton, N. S. (1988). Song discrimination learning in zebra finches. *Animal Behaviour*, *36*(4), 1016–1024. https://doi.org/10.1016/S0003-3472(88)80061-7

Cynx, J., & Nottebohm, F. (1992). Role of gender, season, and familiarity in discrimination of conspecific song by zebra finches (*Taeniopygia guttata*). *Proceedings of the National Academy of Sciences*, *89*(4), 1368–1371.

Daou, A., Johnson, F., Wu, W., & Bertram, R. (2012). A computational tool for automated large-scale analysis and measurement of bird-song syntax. *Journal of Neuroscience Methods*, *210*(2), 147–160.

Derégnaucourt, S. (2011). Birdsong learning in the laboratory, with especial reference to the song of the Zebra Finch (*Taeniopygia guttata*). *Interaction Studies*, *12*(2), 324–350. https://doi.org/10.1075/is.12.2.07der

Derégnaucourt, S., & Gahr, M. (2013). Horizontal transmission of the father's song in the zebra finch (*Taeniopygia guttata*). *Biology Letters*, *9*(4), 20130247. https://doi.org/10.1098/rsbl.2013.0247

Derégnaucourt, S., Poirier, C., Van der Kant, A., Van der Linden, A., & Gahr, M. (2013). Comparisons of different methods to train a young zebra finch (*Taeniopygia guttata*) to learn a song. *Journal of Physiology-Paris*, *107*(3), 210–218.

Derryberry, E. P. (2007). Evolution of Bird Song Affects Signal Efficacy: An Experimental Test Using Historical and Current Signals. *Evolution*, *61*(8), 1938–1945. https://doi.org/10.1111/j.1558-5646.2007.00154.x

Eastzer, D. H., King, A. P., & West, M. J. (1985). Patterns of courtship between cowbird subspecies: Evidence for positive assortment. *Animal Behaviour*, *33*(1), 30–39. https://doi.org/10.1016/S0003-3472(85)80117-2

Elie, J. E., Soula, H. A., Mathevon, N., & Vignal, C. (2011). Dynamics of communal vocalizations in a social songbird, the zebra finch (*Taeniopygia guttata*). *The Journal of the Acoustical Society of America*, *129*(6), 4037–4046. https://doi.org/10.1121/1.3570959

Ey, E., & Fischer, J. (2009). The "acoustic adaptation hypothesis"—A review of the evidence from birds, anurans and mammals. *Bioacoustics*, *19*(1–2), 21–48.

Feher, O., Wang, H., Saar, S., Mitra, P. P., & Tchernichovski, O. (2009). De novo establishment of wild-type song culture in the zebra finch. *Nature*, *459*(7246), 564–568.

Fisher, J., & Hinde, R. A. (1949). The opening of milk bottles by birds. *British Birds*, *42*, 347–357.

Forstmeier, W., Burger, C., Temnow, K., & Derégnaucourt, S. (2009). The genetic basis of zebra finch vocalizations. *Evolution*, *63*(8), 2114–2130.

Fraley, C., & Raftery, A. E. (2006). *MCLUST version 3 for R: Normal mixture modeling and model-based clustering*. Citeseer.

García, N. C., Arrieta, R. S., Kopuchian, C., & Tubaro, P. L. (2015). Stability and change through time in the dialects of a Neotropical songbird, the Rufous-collared Sparrow. *Emu*, *115*(4), 309–316.

Haesler, S., Rochefort, C., Georgi, B., Licznerski, P., Osten, P., & Scharff, C. (2007). Incomplete and Inaccurate Vocal Imitation after Knockdown of FoxP2 in Songbird Basal Ganglia Nucleus Area X. *PLOS Biology*, *5*(12), e321. https://doi.org/10.1371/journal.pbio.0050321

Harbison, H., Nelson, D. A., & Hahn, T. P. (1999). Long-Term Persistence of Song Dialects in the Mountain White-Crowned Sparrow. *The Condor*, *101*(1), 133–148. https://doi.org/10.2307/1370454

Hausberger, M., Bigot, E., & Clergeau, P. (2008). Dialect use in large assemblies: A study in European starling *Sturnus vulgaris* roosts. *Journal of Avian Biology*, *39*(6), 672–682.

Hyland Bruno, J., & Tchernichovski, O. (2017). Regularities in zebra finch song beyond the repeated motif. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2017.11.001

Immelmann, K. (1969). Song development in the zebra finch and other estrildid finches. *Bird Vocalizations*, *61*.

Iyengar, S., & Bottjer, S. W. (2002). The Role of Auditory Experience in the Formation of Neural Circuits Underlying Vocal Learning in Zebra Finches. *Journal of Neuroscience*, *22*(3), 946–958. https://doi.org/10.1523/JNEUROSCI.22-03-00946.2002

Jenkins, P. F. (1978). Cultural transmission of song patterns and dialect development in a free-living bird population. *Animal Behaviour*, *26*, 50–78. https://doi.org/10.1016/0003-3472(78)90007-6

Jones, A. E., & Slater, P. J. B. (1996). The Role of Aggression in Song Tutor Choice in the Zebra Finch: Cause or Effect? *Behaviour*, *133*(1/2), 103–115.

Kao, M. H., & Brainard, M. S. (2006). Lesions of an Avian Basal Ganglia Circuit Prevent Context-Dependent Changes to Song Variability. *Journal of Neurophysiology*, *96*(3), 1441–1455. https://doi.org/10.1152/jn.01138.2005

Kawamura, S. (1954). On a new type of feeding habit which developed in a group of wild Japanese monkeys. *Seibutsu-Shinka*, *2*, 11–13.

King, A. P., West, M. J., & Eastzer, D. H. (1980). Song structure and song development as potential contributors to reproductive isolation in cowbirds (*Molothrus ater*). *Journal of Comparative and Physiological Psychology*, *94*(6), 1028–1039. https://doi.org/10.1037/h0077737

Kirby, S., Cornish, H., & Smith, K. (2008). Cumulative cultural evolution in the laboratory: An

experimental approach to the origins of structure in human language. *Proceedings of the National Academy of Sciences*, *105*(31), 10681–10686.

Lachlan, R. F., & Servedio, M. R. (2004). Song Learning Accelerates Allopatric Speciation. *Evolution*, *58*(9), 2049–2063. https://doi.org/10.1111/j.0014-3820.2004.tb00489.x

Lachlan, R. F., van Heijningen, C. A., ter Haar, S. M., & ten Cate, C. (2016). Zebra Finch Song Phonology and Syntactical Structure across Populations and Continents—A Computational Comparison. *Frontiers in Psychology*, *7*.

Lachlan, R. F., Ratmann, O., & Nowicki, S. (2018). Cultural conformity generates extremely stable traditions in bird song. *Nature Communications*, *9*(1), 2417. https://doi.org/10.1038/s41467-018-04728-1

Lachlan, R. F., Verzijden, M. N., Bernard, C. S., Jonker, P.P., Koese, B., Jaarsma, S., Spoor, W., Slater, P. J. B. & ten Cate, C. (2013). The progressive loss of syntactical structure in bird song along an island colonization chain. *Current Biology*, *23*(19), 1896–1901.

Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, *21*(10), 542–547.

Lansverk, A. L., Schroeder, K. M., London, S. E., Griffith, S. C., Clayton, D. F., & Balakrishnan, C. N. (2019). The variability of song variability in zebra finch (*Taeniopygia guttata*) populations. *Royal Society Open Science*, *6*(5), 190273.

Liu, W., Kohn, J., Szwed, S. K., Pariser, E., Sepe, S., Haripal, B., Oshimori, N., Marsala, M., Miyanohara, A. & Lee, R. (2015). Human mutant huntingtin disrupts vocal learning in transgenic songbirds. *Nature Neuroscience*, *18*(11), 1617–1622. https://doi.org/10.1038/nn.4133

Mammen, D. L., & Nowicki, S. (1981). Individual differences and within-flock convergence in chickadee calls. *Behavioral Ecology and Sociobiology*, *9*(3), 179–186. https://doi.org/10.1007/BF00302935

Marler, P., & Tamura, M. (1962). Song 'Dialects' in Three Populations of White-Crowned Sparrows. *The Condor*, *64*(5), 368–377. https://doi.org/10.2307/1365545

Mennill, D. J., Doucet, S. M., Newman, A. E. M., Williams, H., Moran, I. G., Thomas, I. P., Woodworth, B.K. & Norris, D. R. (2018). Wild Birds Learn Songs from Experimental Vocal Tutors. *Current Biology*, *28*(20), 3273-3278.e4. https://doi.org/10.1016/j.cub.2018.08.011

Mets, D. G., & Brainard, M. S. (2018). Genetic variation interacts with experience to determine interindividual differences in learned song. *Proceedings of the National Academy of Sciences*, *115*(2), 421–426. https://doi.org/10.1073/pnas.1713031115

Mundinger, P. C. (1970). Vocal Imitation and Individual Recognition of Finch Calls. *Science*, *168*(3930), 480–482. https://doi.org/10.1126/science.168.3930.480

Podos, J. (2018). Animal Behavior: Song Learning out of the Box. *Current Biology*, *28*(20), R1195–R1197. https://doi.org/10.1016/j.cub.2018.08.054

Podos, J., & Nowicki, S. (2004). Beaks, adaptation, and vocal evolution in Darwin's finches. *AIBS Bulletin*, *54*(6), 501–510.

Price, P. H. (1979). Developmental determinants of structure in zebra finch song. *Journal of Comparative and Physiological Psychology*, *93*(2), 260–277. https://doi.org/10.1037/h0077553

Riebel, K. (2003). The "Mute" Sex Revisited: Vocal Production and Perception Learning in Female Songbirds. In *Advances in the Study of Behavior* (Vol. 33, pp. 49–86). https://doi.org/10.1016/S0065-3454(03)33002-5

Scharff, C., & Nottebohm, F. (1991). A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: Implications for vocal learning. *Journal of Neuroscience*, *11*(9), 2896–2913. https://doi.org/10.1523/JNEUROSCI.11-09-02896.1991

Searcy, W. A., & Andersson, M. (1986). Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, *17*(1), 507–533.

Sibly, R. M., Nott, H. M. R., & Fletcher, D. J. (1990). Splitting behaviour into bouts. *Animal Behaviour*, *39*(1), 63–69. https://doi.org/10.1016/S0003-3472(05)80726-2

Slater, P. J. B., & Clayton, N. S. (1991). Domestication and song learning in zebra finches *Taeniopygia guttata*. *Emu-Austral Ornithology*, *91*(2), 126–128.

Slater, P. J. B., & Lester, N. P. (1982). Minimising Errors in Splitting Behaviour Into Bouts. *Behaviour*, *79*(2–4), 153–161. https://doi.org/10.1163/156853982X00229

Tchernichovski, O., Feher, O., Fimiarz, D., & Conley, D. (2017). How social learning adds up to a culture: From birdsong to human public opinion. *Journal of Experimental Biology*, *220*(1), 124–132. https://doi.org/10.1242/jeb.142786

Tchernichovski, O., & Lipkind, D. (2016). Encoding vocal culture. *Science*, *354*(6317), 1234–1235. https://doi.org/10.1126/science.aal3205

Tchernichovski, O., & Nottebohm, F. (1998). Social inhibition of song imitation among sibling male zebra finches. *Proceedings of the National Academy of Sciences*, *95*(15), 8951–8956.

Tchernichovski, O., Nottebohm, F., Ho, C. E., Pesaran, B., & Mitra, P. P. (2000). A procedure for an automated measurement of song similarity. *Animal Behaviour*, *59*(6), 1167–1176. https://doi.org/10.1006/anbe.1999.1416

Temeles, E. J. (1994). The role of neighbours in territorial systems: When are they 'dear enemies'? *Animal Behaviour*, *47*(2), 339–350. https://doi.org/10.1006/anbe.1994.1047

Trainer, J. M. (1983). Changes in Song Dialect Distributions and Microgeographic Variation in Song of White-Crowned Sparrows (*Zonotrichia leucophrys nuttalli*). *The Auk*, *100*(3), 568–582. https://doi.org/10.1093/auk/100.3.568

Whitney, C. L. (1992). Temporal stability of song in a local population of Wood Thrushes. *The Wilson Bulletin*, *104*(3), 516–520.

Williams, H. (1990). Models for song learning in the zebra finch: Fathers or others? *Animal Behaviour*, *39*(4), 745–757. https://doi.org/10.1016/S0003-3472(05)80386-0

Wu, W., Thompson, J. A., Bertram, R., & Johnson, F. (2008). A statistical method for quantifying songbird phonology and syntax. *Journal of Neuroscience Methods*, *174*(1), 147–154. https://doi.org/10.1016/j.jneumeth.2008.06.033

Zann, R. A. (1993). Variation in song structure within and among populations of Australian zebra finches. *The Auk*, 716–726.

Zann, R. A. (1996). *The zebra finch: A synthesis of field and laboratory studies* (Vol. 5). Oxford University Press.

Zevin, J. D., Seidenberg, M. S., & Bottjer, S. W. (2004). Limits on reacquisition of song in adult zebra finches exposed to white noise. *Journal of Neuroscience*, *24*(26), 5849–5862.

SUPPLEMENTAL INFORMATION

Supplementary figures

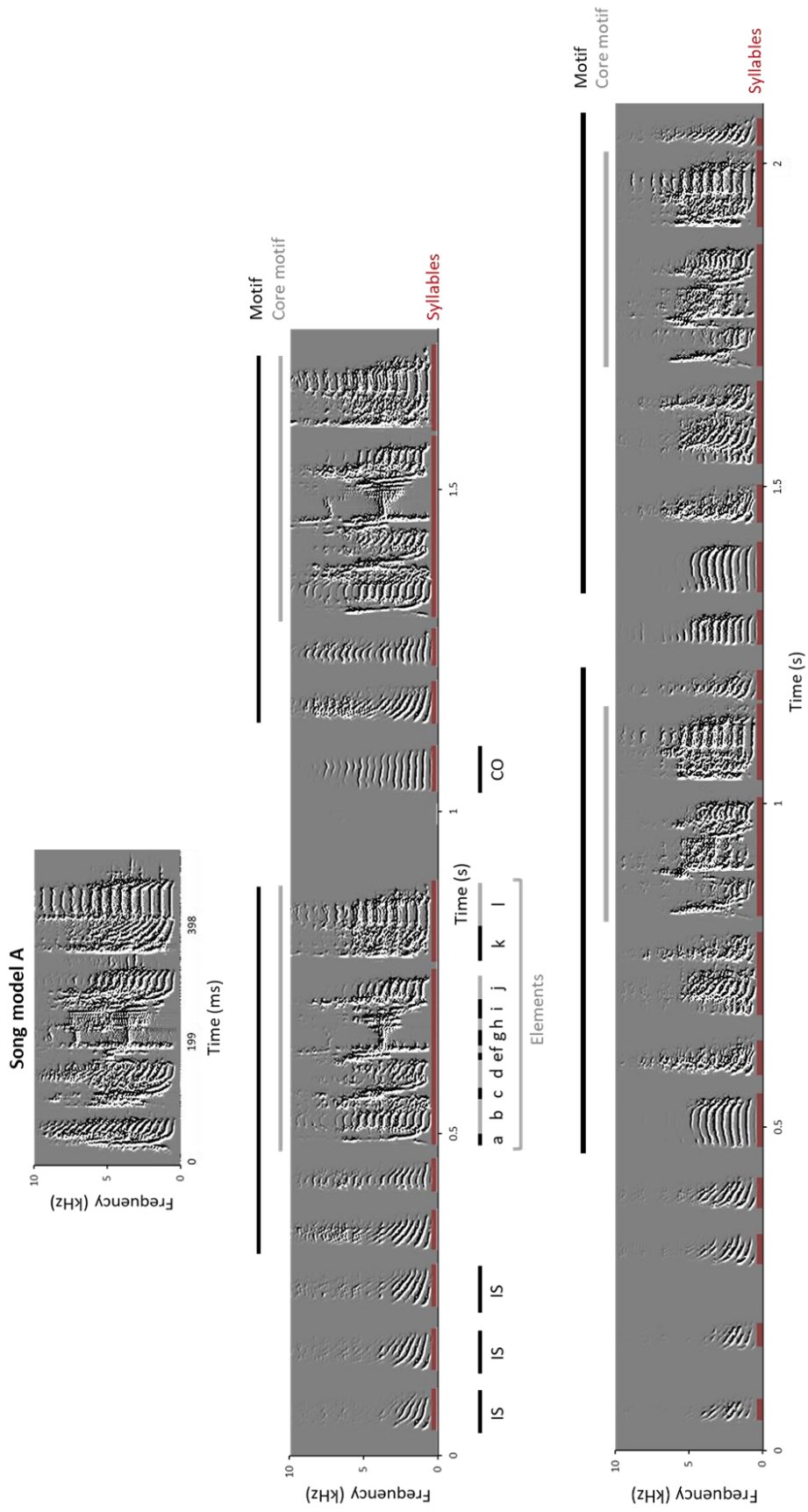


Figure S1. Song organization in the zebra finch

In this spectrogram, the different units of a typical zebra finch song described in the main text and in STAR Methods are indicated: Syllables are underlined in red, core motifs are overlined in grey and motifs in black. IS indicates "Introductory Syllables" and CO indicates "Connector". Cursive letters from *a* to *l* indicate the different elements of a core motif.

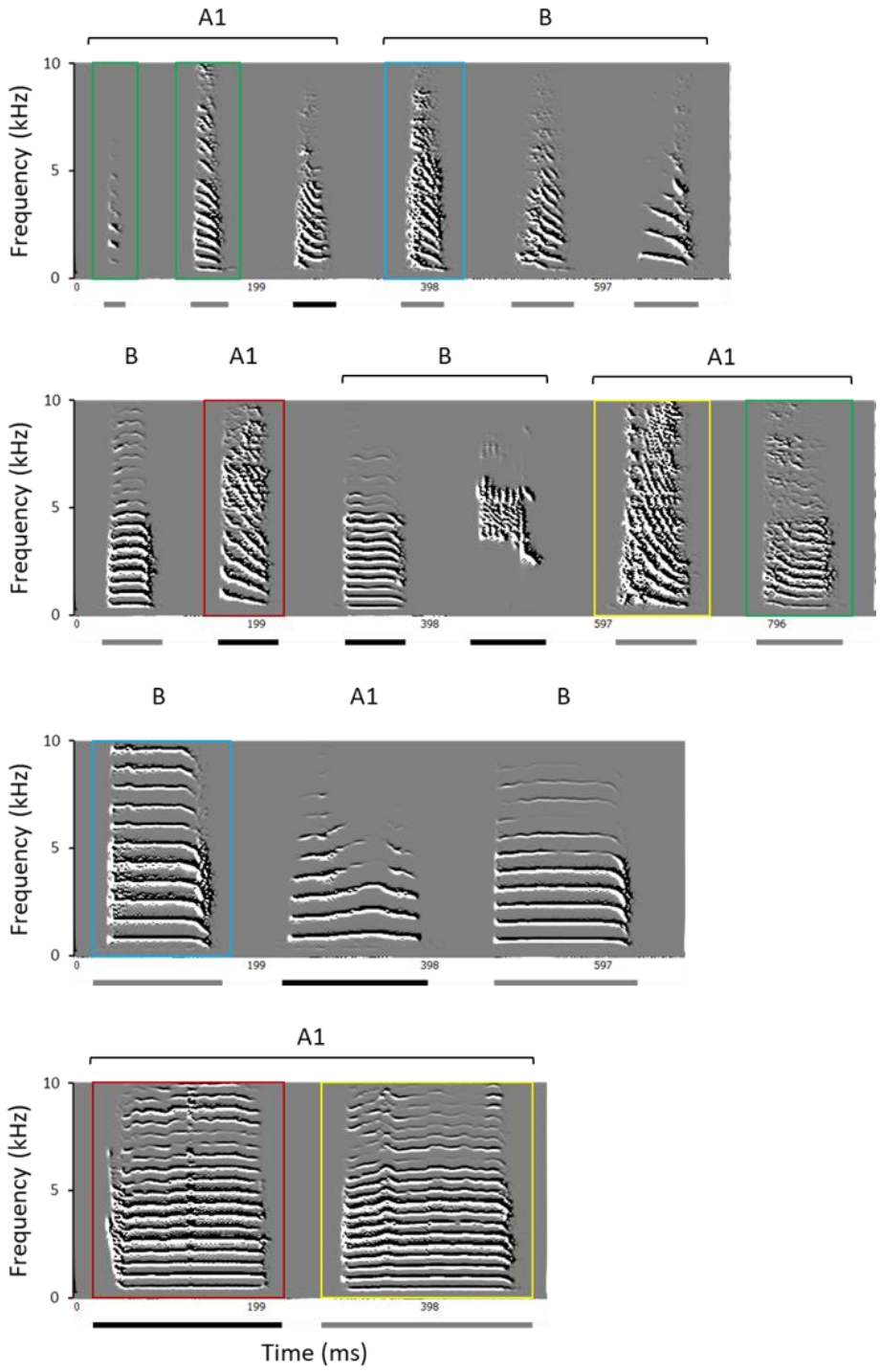


Figure S2. Example spectrograms of connector types produced by birds of colony A1 and colony B

We observed a high intra- and inter-individual variability in the connector types that were produced by birds: above each connector type is indicated from which colony comes the male that produced it (colony A1 or B); connectors underlined in black were produced by founder males and connectors underlined in grey were produced by male offspring; connectors that were produced by the same individual are framed by rectangles of the same colour.

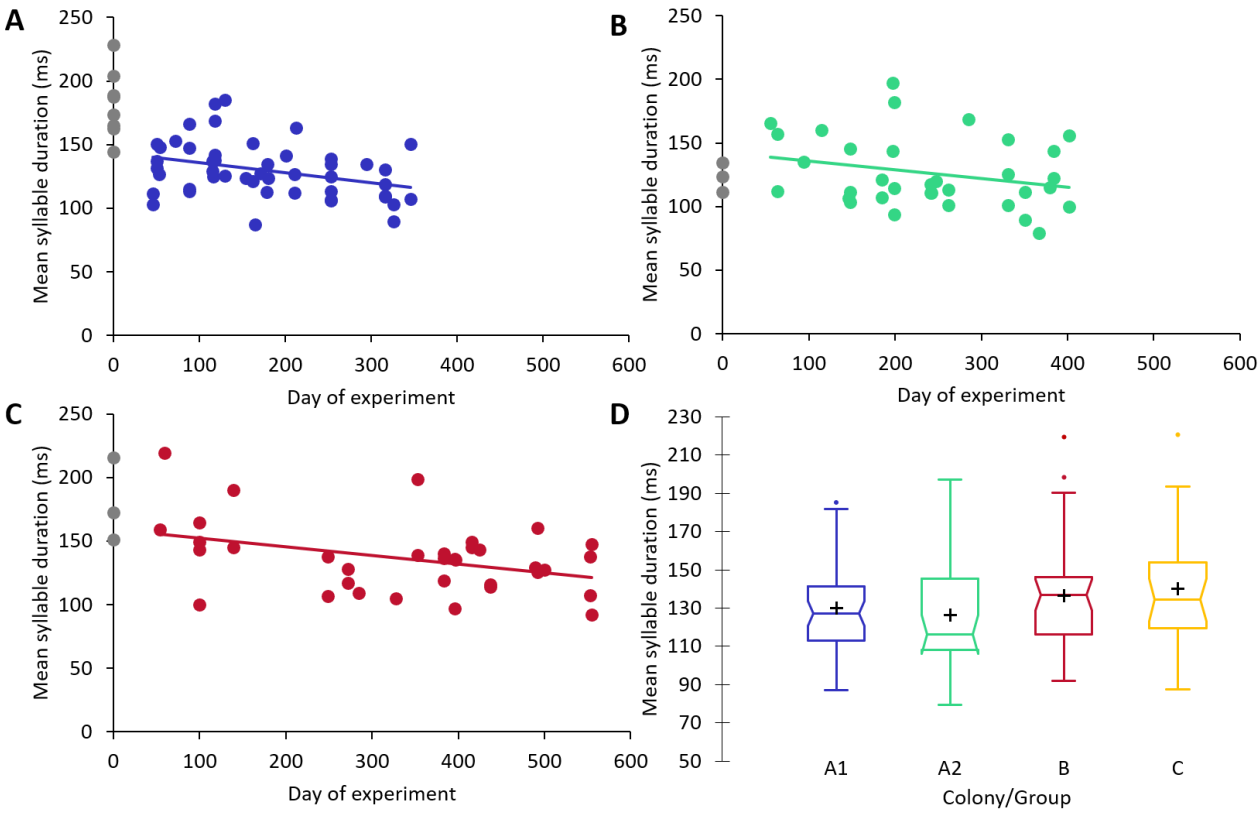


Figure S3. Changes of syllable duration over time in the three colonies and comparison between groups

(A) Mean syllable duration significantly decreased over time in colony A1 (r_s = -0.321, p = 0.026).

(B) Mean syllable duration did not decrease significantly over time in colony A2 (r_s = -0.227, p = 0.195).

(C) Mean syllable duration did not decrease significantly over time in colony B (r_s = -0.295, p = 0.085).

In panel (A), (B) and (C), grey dots represent founder males. On the x-axis, each male is represented according to his hatching day in reference to the day of the experiment, day 0 of the experiment being the day when male founders were introduced into the aviary with naive females.

(D) There were no significant group differences in the mean syllable duration ($\chi 2$ = 4.43; d.f. = 3; p = 0.218). Box-and-whisker plots depict the median, interquartile range and non-outlier range (whisker length up to 1.5 times the interquartile range). Crosses indicate mean values.

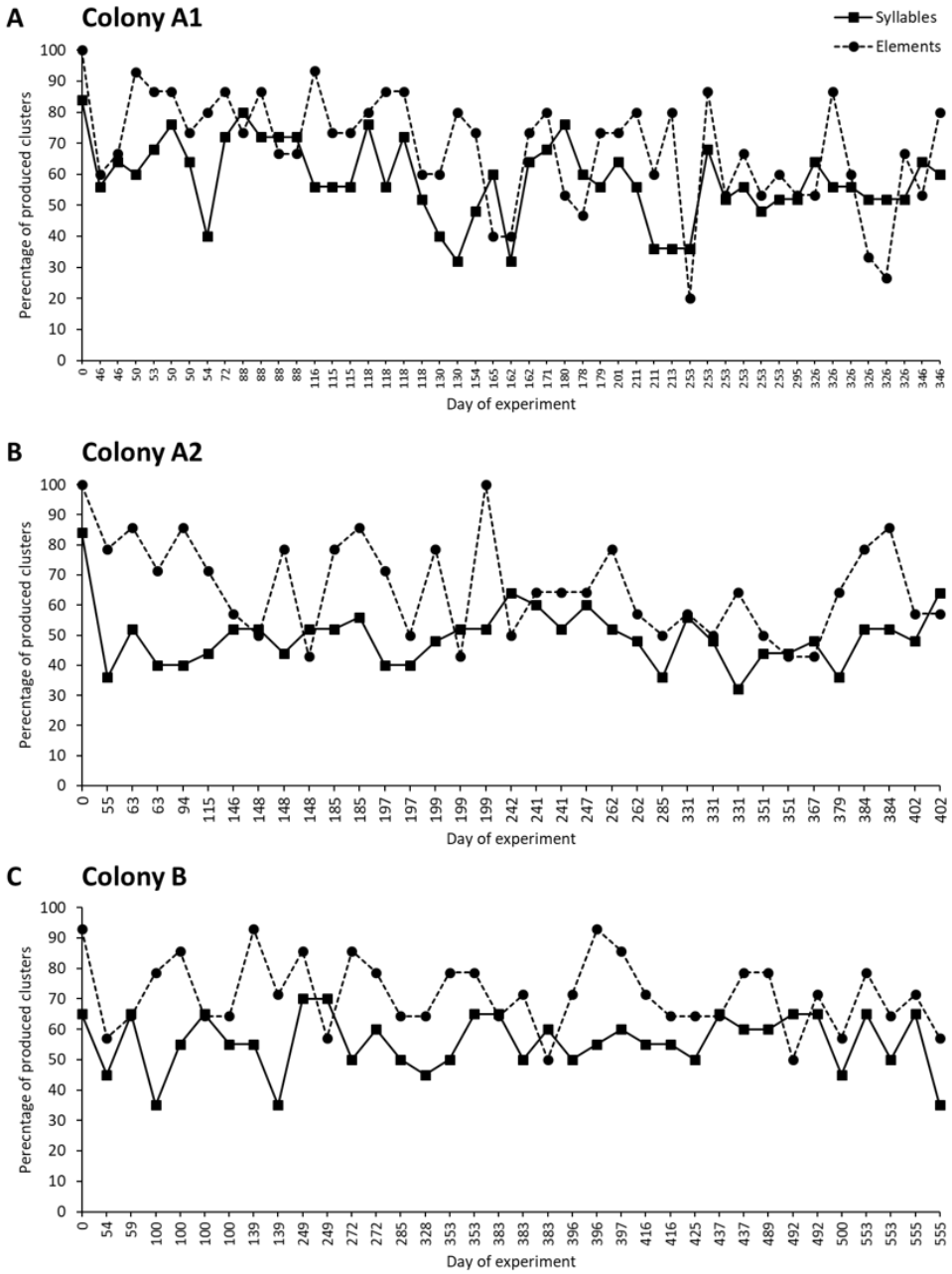


Figure S4. High inter-individual variability in the production of syllable and element types
Percentage of produced syllable and element clusters over time in colony A1 (A), colony A2 (B) and colony B (C). On each graph, the zero value on the *x*-axis represents the percentage for all of the founders (i.e. in colony A1, 100% of the colony's element types were produced by the founder males). There was a decrease of element types production over time in colony A1 (r_s = -0.45, p = 0.0015) and A2 (r = -0.34, p = 0.04), but not in colony B (r_s = -0.142, p = 0.412). On the *x*-axis, each male is represented according to his hatching day in reference to the day of the experiment, day 0 of the experiment being the day when male founders were introduced into the aviary with naive females.

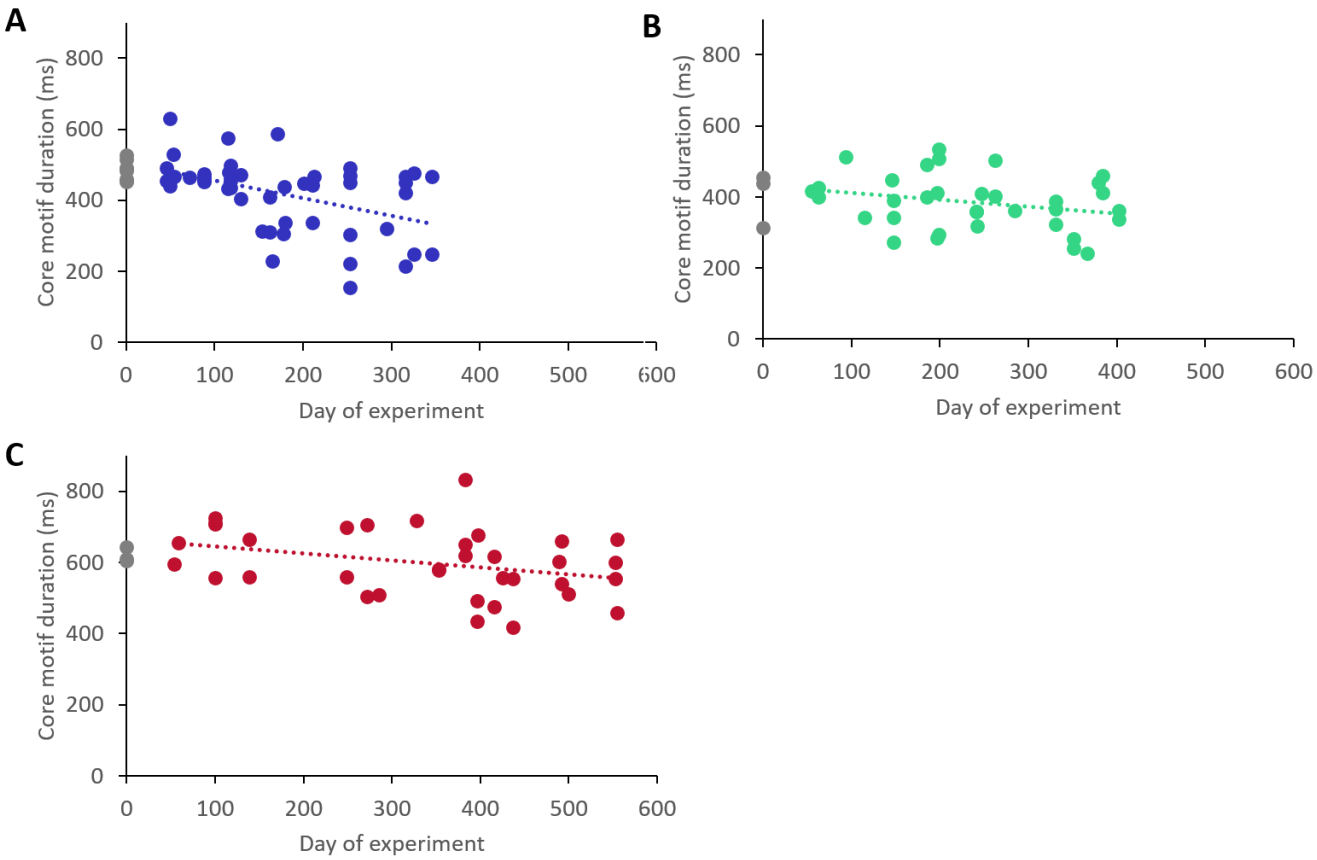


Figure S5. Changes of core motif duration over time in the three colonies

(A) Core motif duration significantly decreased over time in colony A1 (r_s = -0.414, p = 0.003).

(B) Core motif duration did not significantly decrease over time in colony A2 (r = -0.267, p = 0.126).

(C) Core motif duration significantly decreased over time in colony B (r_s = -0.386, p = 0.022).

Grey dots represent founder males. On the *x*-axis, each male is represented according to his hatching day in reference to the day of the experiment, day 0 of the experiment being the day when male founders were introduced into the aviary with naive females.

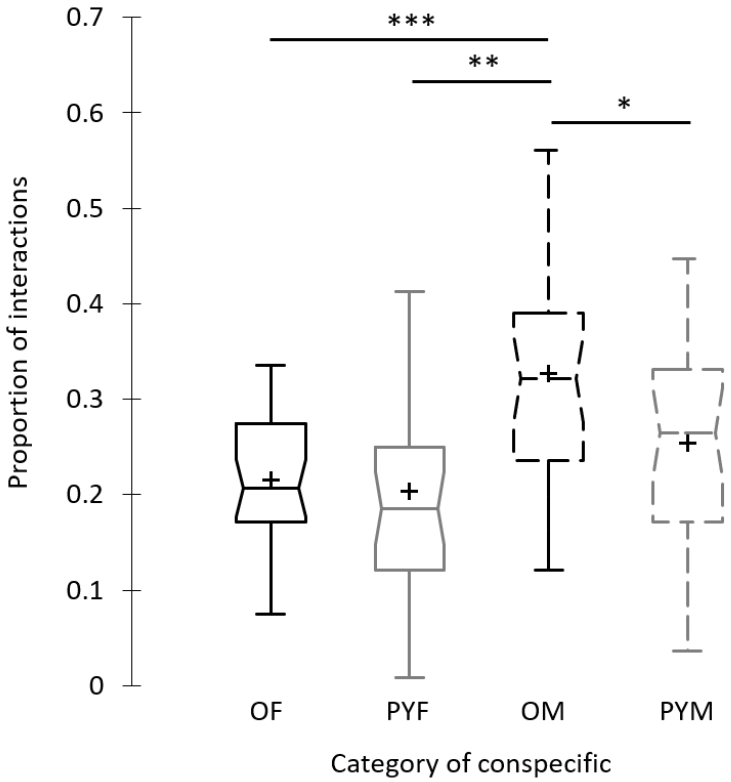


Figure S6. Pupils of colony A2 interacted more with older males

There was a significant difference between the proportion of interactions with the four categories of conspecifics: older females (OF), peer or younger females (PYF), older males (OM) and peer or younger males (PYM) ($\chi^2 = 17.9$, df = 3, $p < 0.001$).

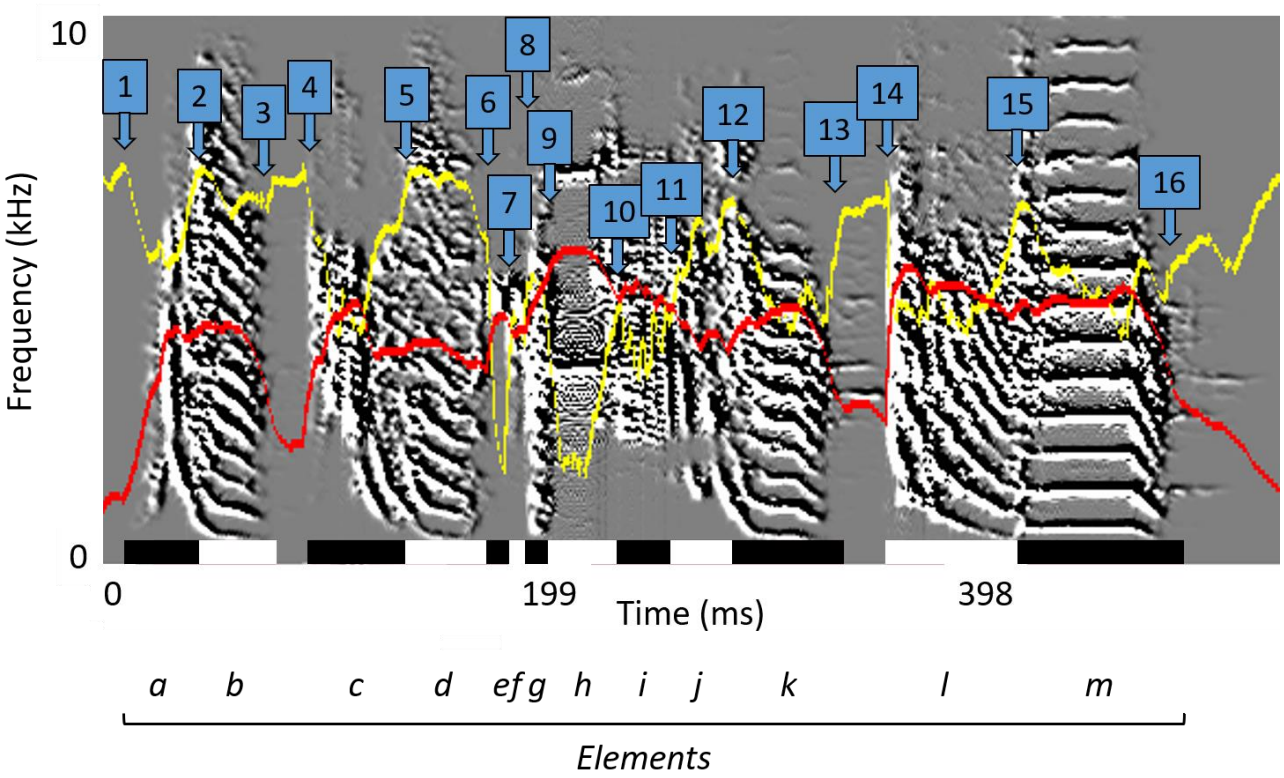


Figure S7. Spectrographic illustration of time events and elements in the song model A (core motif)

Each number represents a different time event characterised by abrupt changes in amplitude (red curve) and entropy (yellow curve). The black and white bars at the bottom of the spectrogram and the corresponding letters from *a* to *m* indicate the different elements delineated by the time events.

Supplementary tables

Table S1. No significant changes of linearity, consistency and stereotypy over time in the song bouts of the three colonies

The linearity, consistency and stereotypy score of each male is not correlated with the day of experiment he hatched (day 0 of the experiment being the day when male and female founders were introduced into the aviary).

			Correlation between hatching day and:		
Colony	N		Linearity	Consistency	Stereotypy
A1	48	r_s	0.074	0.076	0.082
		p - value	0.617	0.606	0.581
A2	34	r_s	-0.009	-0.177	-0.063
		p - value	0.958	0.317	0.721
B	35	r_s	0.087	0.045	0.084
		p - value	0.614	0.798	0.63

Table S2. Summary of the number of syllable and element clusters found in each group

The total number of syllable clusters found after clustering analysis was 26. The total number of element clusters found after clustering analysis was 15.

Colony or group	Number of syllable clusters	Number of element clusters	Number of syllable clusters found in founders' song	Number of element clusters found in founders' song
A1	25	15	21	15
A2	25	14	21	14
B	20	14	13	13
C	21	15	not applicable	not applicable

Table S3. Dwass-Steel-Critchlow-Fligner pairwise comparisons of PC1 scores of K-L distances

Significant outcomes are given in bold.

Pairwise comparison	W	*p - value*
A1 – A2	0.537	0.981
A1 – B	8.574	**< 0.001**
A1 – C	-19.435	**< 0.001**
A2 – B	7.570	**< 0.001**
A2 – C	-18.167	**< 0.001**
B – C	-21.641	**< 0.001**

Table S4. Games-Howell post-hoc test for pairwise comparisons on the mean number of connector types per song bout

Significant outcomes are given in bold.

		A2	B	C
A1	Mean difference	-0.665	1.07	0.831
	t - value	-1.92	4.32	2.618
	df	66.6	75.5	56.2
	p - value	0.231	**< 0.001**	0.054
A2	Mean difference		1.74	1.495
	t - value		5.67	4.104
	df		47.6	55.9
	p - value		**< 0.001**	**< 0.001**
B	Mean difference			-0.243
	t - value			-0.893
	df			37.2
	p - value			0.808

Table S5. Dwass-Steel-Critchlow-Fligner pairwise comparisons of mean number of elements per core motif

Significant outcomes are given in bold.

Pairwise comparison	W	*p – value*
A1 – A2	-1.046	0.881
A1 – B	7.184	< **0.001**
A1 – C	0.808	0.941
A2 – B	6.708	< **0.001**
A2 – C	1.042	0.882
B – C	-2.838	0.186

Table S6. Wilcoxon signed rank test for pairwise comparisons of proportion interactions with different conspecific categories in colony A2

There are four categories of conspecifics: older females (OF), peer or younger females (PYF), older males (OM) and peer or younger males. Significant outcomes are given in bold.

Pairwise comparisons	V	*p - value*
OF – PYF	211	0.605
OF – OM	21	< **0.001**
OF – PYM	137.5	0.139
PYF – OM	70	**0.002**
PYF – PYM	137	0.136
OM – PYM	311	**0.043**

Table S7. Number and training method for male founders of the three colonies

Colony	Song model	Number of founders	Origin	Training method	Number per training method
A1	A	10 (8)	Max Planck Institute of Ornithology – Seewiesen, Germany	Operant conditioning	4
				One to one live tutoring	2
				Multiple tutors producing imitations of the same song model (aviary)	4
A2	A	3	Laboratoire Ethologie Cognition Développement – Nanterre, France	Multiple tutors (from colony A1)	3
B	B	3	Laboratoire Ethologie Cognition Développement – Nanterre, France	Operant conditioning	3

Table S8. List of social behaviours observed in the colonies

Behaviour	Nature of behaviour
aggressive pecking	agonistic
allopreening	affiliative
approaching	affiliative
avoiding	agonistic
beak fencing	agonistic
beak wiping	affiliative
being close to a conspecific	neutral
body contact	affiliative
chasing	agonistic
clumping	affiliative
courtship	affiliative
courtship song	affiliative
defended against a third party	affiliative
directed song	affiliative
feather plugged	agonistic
feeding close to a conspecific	affiliative
following	affiliative
greeting	affiliative
inspecting nest	affiliative
invitation allopreening	affiliative
jump on the back	neutral
listening to the song	affiliative
monopolising feeding ground	agonistic
observing beak fence	neutral
mandibulating (quick opening/closing of mandibles)	agonistic
neutral pecking	neutral
receiving directed song	affiliative
singing at	affiliative
singing with	affiliative
soft peck	affiliative
steal nest material	agonistic
threat	agonistic
try to steal nest material	agonistic
went in between two conspecifics	affiliative
wing strokes	affiliative

Table S9. Original table of classifications resulting from the Discriminant Function Analysis (DFA) and leading to a model accuracy of 76%

Predicted \ Actual	A1	A2	B	C
A1	43	13	2	3
A2	8	21	0	5
B	3	0	36	1
C	2	0	0	15

Supplementary data

Multiple versions of the song motif

Some males produced up to three different versions of the core motif. In colony A1, four founder males had two different versions of the core motif and one had three versions. 18 pupils had two versions and four of them had three. In colony A2, only one founder male and five pupils produced two different versions of the core motif. In colony B, two founder males and nine pupils had two different versions of core motif and only one pupil had three versions.

Artificial dialects - DFA analysis

The original DFA analysis on core motifs led to a model accuracy of 76% (Table S9). Some motifs have been classified in colony A2 when they actually should have been in colony A1 and vice versa. However, given that males of the colonies A1 and A2 sang imitations of the same song model, we cannot consider these cases as misclassifications. Thus, we modified the table accordingly and this modified table of classifications led to a model accuracy of 89% (Table 1).

Analysis of social interactions

Overall, we described 22,819 social interactions (10,564 in colony A2 and 12,255 in colony B). However, for the final analysis we kept only dyadic interactions and excluded some behaviours such as parental behaviours (feeding and begging). That left us with 6,410 dyadic interactions (colony A2: n = 2,672; colony B: n = 3,738).

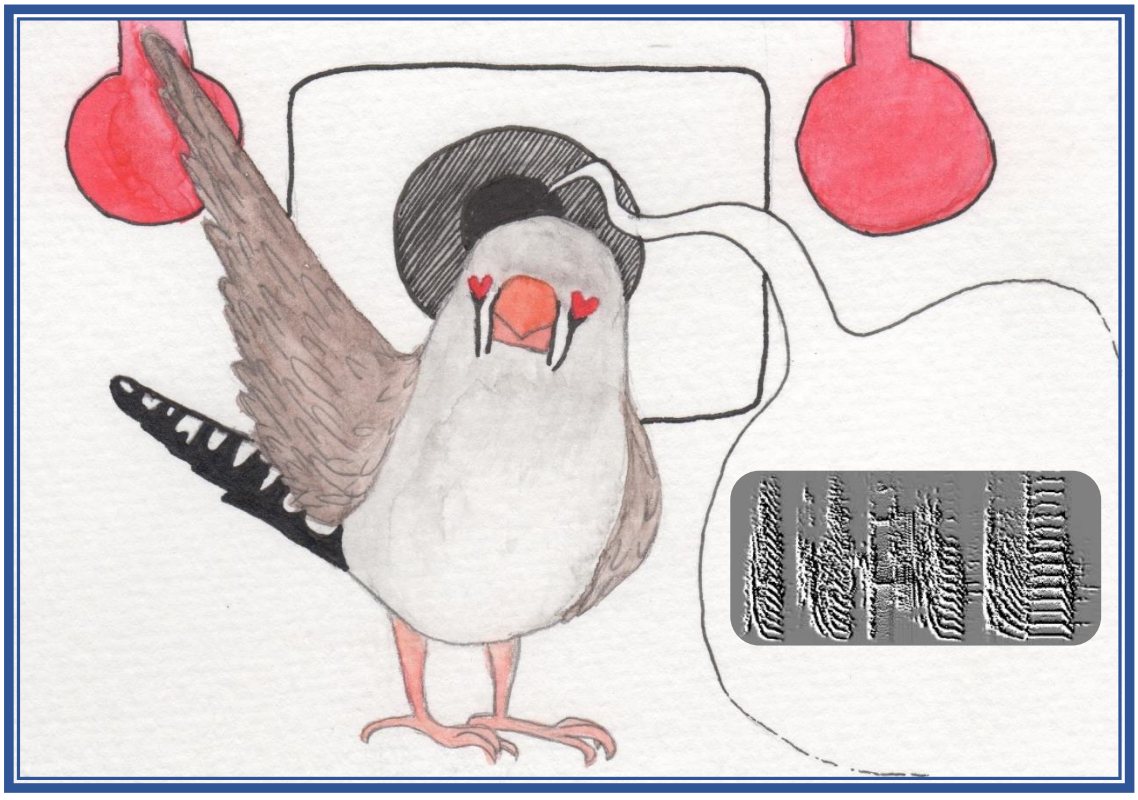
As the number of available interactors significantly increased over time in both colonies (colony A2: $r = 0.715$, $p < 0.001$; colony B: $r_s = 0.823$, $p < 0.001$), we could not take into account the absolute number of interactions or interactors. Thus, we based our first analysis on

proportions. When correlating social interactions with indicators of song learning (similarity scores), the number of individuals was reduced to 31 individuals in colony B, as 5 observed pupils died before their song could be recorded.

In order to also consider absolute numbers of interactions we conducted another analysis solely on the major interactor per pupil. To examine whether interactions with the major interactor had an influence on how well the subject had imitated the song of his major interactor, we calculated a similarity score between the core motif of the pupil and the one of his major interactor. We used the same technique as described before (see section “similarity score”). In SAP 2011, the core motif of the major interactor was used as the model and the core motif of the pupil was compared to this model. For males that had several core motif versions, we considered only the version that revealed the highest similarity score between a pupil and his major interactor. This is justified by the fact that a pupil could have imitated preferentially the second core motif of his major interactor.

⁎ Chapter II ⁎

Female preference for artificial song dialects in the zebra finch (*Taeniopygia guttata*)



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Female preference for artificial song dialects in the zebra finch (*Taeniopygia guttata*)

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ABSTRACT

Birdsong is culturally transmitted and geographical variations of song have been found in several songbird species. There is evidence that such dialects contribute to reproductive isolation through variation in female preference. In the wild, there is no report of consistent dialects in populations of zebra finches. However, under laboratory conditions, we were able to create artificial song dialects. In this species, song plays a crucial role in mate choice and the importance of subadult song experience in shaping adult song preferences has been well documented. Therefore, we expected females to prefer songs corresponding to their colony's dialect. We measured this preference using an operant test: females could either trigger a song corresponding to their Colony Song Type (CST) sang by an unfamiliar individual, or another conspecific song, corresponding to a Non-Colony Song Type (N-CST). Most females preferred the CST over the N-CST, supporting the idea that zebra finch females exhibit a preference for the song they heard early in life. It also reveals that song dialects matter to female zebra finches. It has been proposed that song could be used as an affiliative signal in highly social species. Therefore, preferring the colony dialect could be the consequence of a sexual preference, but it could as well be the consequence of a social preference. We discuss the potential role of song dialects in the context of social learning.

Keywords: female preference, dialects, birdsong, operant test, zebra finch

CHAPTER II

INTRODUCTION

Birdsong has been studied for decades and is known to be a multifaceted signal with various functions. In many species, it has been demonstrated that mate attraction and stimulation is one of its main functions (Andersson, 1994; Catchpole & Slater, 2008; Slater et al., 1988). For example, females show a preference for songs with specific characteristics such as a large song repertoire, a high song rate or a high amplitude song (Kroodsma, 1976; Ritschard et al., 2010; Searcy, 1992; Searcy & Andersson, 1986; Wasserman & Cigliano, 1991). It has been proposed that such song specificities might be costly and would thus constitute a good indicator of mate quality (Gil & Gahr, 2002; Kroodsma, 1976; Zahavi, 1975; but see Zollinger et al., 2011). In many species, males of a same geographical location sing the same song type or share a substantial part of their song repertoire whereas males of different locations vary in their songs (Podos & Warren, 2007). Such vocal geographical variations can lead to song dialects and can be maintained over very long periods of time (Derryberry, 2007; Garcia et al., 2015; Harbison et al., 1999; Marler & Tamura, 1962; Trainer, 1983). Several hypotheses about the functions of dialects have been proposed (Catchpole & Slater, 2008). According to the hypothesis of "genetic adaptation", geographical variation of birdsong would allow individuals to recognize and mate with individuals of the same population, promoting the maintenance and development of local adaptations (MacDougall-Shackleton & MacDougall-Shackleton, 2001; Marler & Tamura, 1962, 1964; Nottebohm, 1969, 1972). Geographic variation in song could thus influence female mating preferences (Catchpole & Slater, 2008; Searcy & Yasukawa, 1996), with females preferring males singing their natal or local song dialect (King et al., 1980; MacDougall-Shackleton et al., 2001; O'Loghlen & Rothstein, 1995; Searcy & Andersson, 1986). According to the "social adaptation" hypothesis, song dialects affect social and sexual interactions, but dialectal populations should not be genetically isolated from each other (Payne, 1981). Some studies show indeed a positive correlation between vocal sharing and the

maintenance of a territory and/or the reproductive success (Beecher et al. 2000, Payne, 1982, 1983). Song dialects may also play an important role for group cohesion as they may signal group identity (Briefer et al., 2008; Hausberger et al., 2008). For example, it has been shown that song could increase social cohesion in highly social species, such as the European starling (*Sturnus vulgaris*; Hausberger et al., 2008).

Singing behaviour is often sexually dimorphic, as many sexually selected traits. This is the case in the zebra finch (*Taeniopygia guttata*), a highly social species in which only males sing. Young zebra finches learn their song by listening, memorizing and reproducing the song of conspecifics, mainly adults. This song learning takes place during a sensitive period of the early life, between 25- and 90-days post-hatch (dph), and past these 90 days, only few vocal changes are observed (Immelmann, 1969). In the zebra finch, song also plays a crucial role in mate choice and the link between song and female preference has been widely studied (for a review, see Riebel, 2009). Under natural conditions, each male zebra finch has a unique song, which constitutes an individual signature (Clayton, 1988; Cynx & Nottebohm, 1992) and is recognized by the sexual partner (Clayton, 1988). Female zebra finches also have a sensitive phase for song preference learning (Riebel, 2003) and the importance of subadult song experience in shaping adult song preferences has been well demonstrated: if deprived of adult song during the sensitive phase of their early life, females fail to discriminate differences in song quality and do not have consistent choices as adults (Lauay et al., 2004; Riebel, 2000). Females, when adult, do prefer the song they heard when they were young over other songs (Clayton 1988, 1990; Miller 1979a, 1979b; Riebel, 2009). In the wild, females' mate choice is based on different signal modalities, but it has been demonstrated that the song could potentially provide sufficient information about the male for females to assess his quality and allow them to make their choice (Holveck & Riebel, 2007). However, within a same population, females can differ in their preferences. For example, differences between direct benefits (such as

parental care or access to resources) and indirect benefits (inheritance of genes for viability), can lead to differences in female preference (Candolin, 2003). In addition, female preferences can be influenced by social factors such as male/male and female/female competition (Jennions & Petrie, 1997; Widemo & Saether, 1999). It has also been suggested that zebra finch females might rank male signals differently in preference tests, or that no single trait might signal the absolute quality of a male (Holveck & Riebel, 2007).

Until now, studies focusing on zebra finches suggested that dialects could not emerge in this species. Only weak geographical song variations have been found in different Australian populations (Zann, 1993) and it has been concluded that dispersal to and from colonies prevented the formation of colony-specific versions of the song (Zann, 1993). In domesticated populations of zebra finches, a high rate of learning errors probably prevents the establishment of song dialects (Lachlan et al., 2016). However, in our laboratory, we managed to create artificial song dialects by training male founders of three different colonies to produce a very good imitation of a song model (see chapter I of this thesis). Thereby, male pupils that hatched and were raised in such colonies developed songs with a high conformity to the song model, and each song model led to a different dialect (Derégnaucourt et al., 2014; see chapter I of this thesis). Female offspring raised in those colonies heard different versions of a unique song type during their early life: the song dialect of their colony. These conditions allowed us to test for a possible link between song dialects and female preference in a widely studied species. Given that female zebra finches prefer songs they heard when they were young, we predicted that in each colony, females should prefer songs that resemble those produced by males of their colony.

MATERIAL AND METHODS

1) Subjects and rearing conditions

All subjects in this experiment were adult female zebra finches that hatched and were raised in our laboratory. Tested females originated from three different colonies, each of them founded by males originally trained to produce the same song model (see chapter I of this thesis). Two colonies were founded by males singing the song model A (Figure 1A): colony A1 and colony A2. The third colony (colony B) was founded by males singing a different song model, the song model B (Figure 1A).

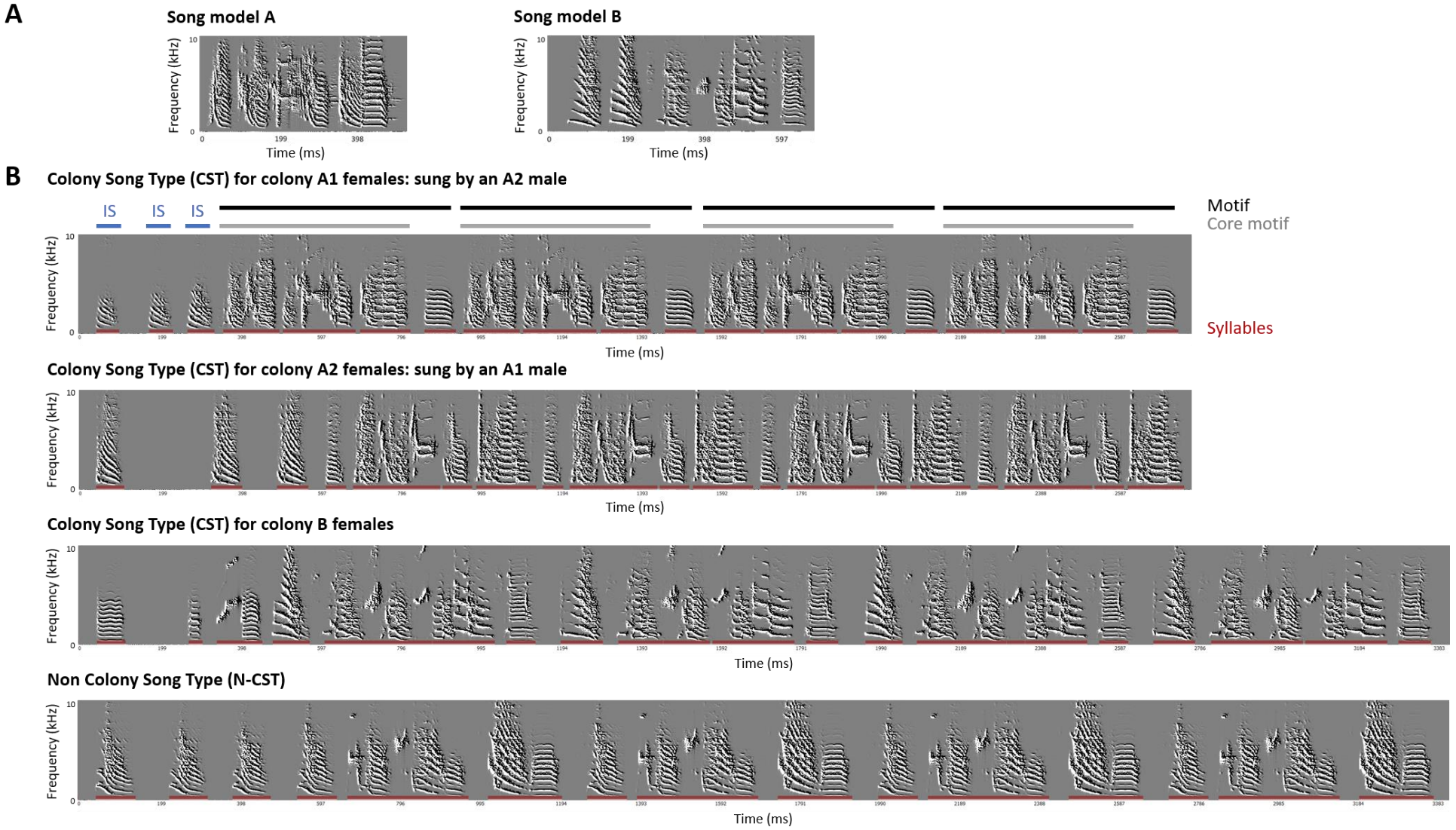

Figure 1. Spectrograms of colonies' song models and of songs used as stimuli for the experiment. (A) Spectrograms of song model A and B that led to specific song dialects. (B) Example of one song set (set #3), composed of four different song stimuli. Each tested female was exposed to two song stimuli within the song set: one Non-Colony Song Type (N-CST) and one Colony Song Type (CST). Females with the same song set were exposed to a different CST stimulus according to their colony. In the first spectrogram (CST for colony A1 females: sung by an A2 male), the different units of a typical zebra finch song are indicated. Syllables are underlined in red, core motifs are overlined in grey and motifs in black. Introductory syllables (IS) are overlined in blue.

Founder females were sexually naive upon colony foundation, as they were isolated from males in a rearing room with their mother alone, from a few days after hatching onwards. When adult, founder males and founder females of each colony were placed together in an aviary containing nest boxes and nesting material, so that they could reproduce freely. For colony A1, we used ten founder males and ten founder females, and we obtained a total of 48 males and 27 females after 400 days of breeding in a communal aviary. For each of the two other colonies (A2 and B), we used three founder males and three founder females (see chapter I of this thesis). In colony A2 we obtained 34 males and 26 females over a 400 days period. In colony B we obtained 38 males and 37 females over 555 days. Birds were individually identified with one red numbered leg band on one leg and two individually differently coloured leg bands, one on each leg. All birds that hatched in those three colonies (including females used for this study) could interact freely with all the other birds of their colony. The three colonies were kept in three different aviaries (3.18 x 3.32 x 2.84 m), visually and acoustically isolated from each other so that the birds could not hear other songs than the songs produced by the males of their colony. All aviaries were set to a 14:10 light:dark (LD) schedule and maintained between 20 and 23°C. Birds had *ad libitum* access to water, seeds mix and egg food for exotic finches, as well as sand and cuttlebones. The basic diet was supplemented once a week with vegetables and fruits, and once a month with hard-boiled eggs.

We tested a total of 63 females: 11 from colony A1, 21 from colony A2 and 31 from colony B. Females from colony A1 were tested at the age of 1,601 ± 86 days post-hatch (dph), females of colony A2 at 792 ± 106 dph and females of colony B at 655 ± 89 dph.

2) Apparatus

We tested the preference of females for their colony's dialect by using an operant task with song as a reward (Riebel, 2000; Riebel et al., 2002; Riebel & Slater, 1998; Salvin et al.,

2018). The experimental operant test set-up has been inspired by the one described in Houx & ten Cate (1999) and used in other studies (Riebel, 2000; Riebel et al., 2002; Salvin et al., 2018). A metal cage (46 x 22 x 26 cm) contained two perches separated by 36 cm. A red response key (1 cm in diameter) was placed above each perch. Behind each key, a mirror of 10 cm diameter was placed to reduce the impact of social isolation. In the centre of the cage floor, we put one food cup (containing seeds and egg food) and one sand cup as well as a water fountain so that food, water and sand were available *ad libitum* throughout the experiment. When pecked, each red key triggered the playback of a different song, played through a loudspeaker (Yamaha MS101 III, Frequency Response: 30 Hz - 20 kHz) placed in between the two response keys. Songs were played at a maximum amplitude of 70 dB at 30 cm from the speaker (Roline R0-1350 sound-level meter; fast response F and low range LO, A settings). This level is comparable to that produced by a singing male (Houx & ten Cate, 1999). Each cage was placed in a sound proof chamber (85 x 65 x 60 cm) equipped with fans providing a low airflow in the chamber and OSRAM DULUX lights on an automatic 14:10 LD schedule.

After manually assigning one specific song to a particular key in SAP 2011 (Sound Analysis Pro software; Tchernichovski et al., 2000), an automated procedure implemented on this software controlled the playback and automatically switched songs between the two keys each night, to control for possible side preferences. This device kept track of all pecks (number of pecks and identity of the key pecked) and stored this information in My SQL Workbench 6.3 CE tables, from which we could extract excel files. This allowed us to track females' progress day by day. Used software ran on a DELL Optilex 9020 PC on Windows 7. Response keys were connected to the computer using a National Instruments USB-6501 port. In order to check whether females intentionally pecked the keys during the test, each sound box was equipped with a Logitech C920 webcam, connected to ContaCam 4.9.9 software on another DELL Optilex 9020 computer. For a representation of the experimental set-up, see Figure 2A.

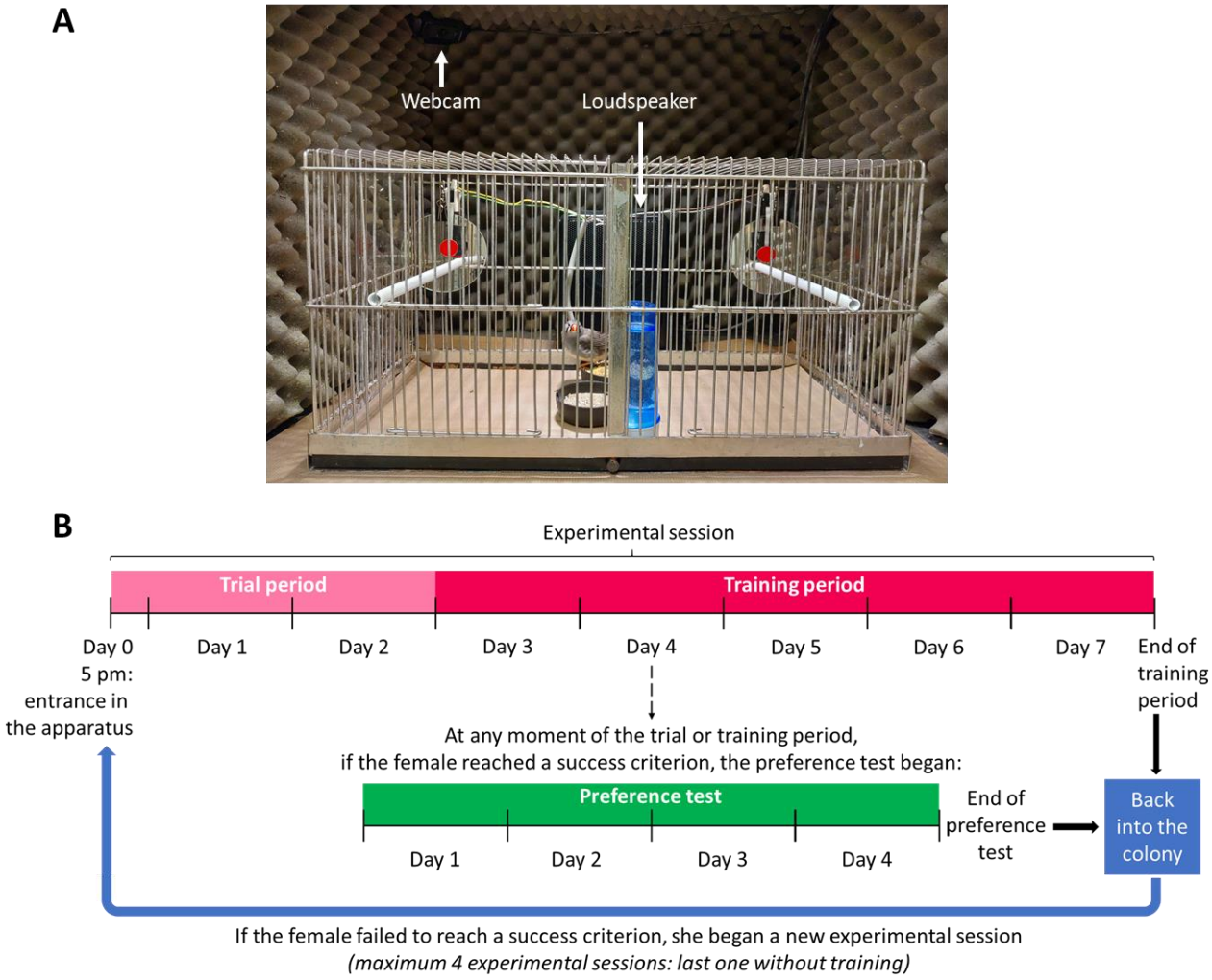

Figure 2. Experimental apparatus and timeline. (A) Experimental set-up for the preference test. (B) Experimental timeline for all females, housed in colony aviaries or in a rearing room until relocation to acoustic chambers for the experimental session.

3) Stimuli

During the test, a female had the possibility to trigger two different song types: one response key triggered the playback of the song type of her colony, which we refer to as the "Colony Song Type" (CST), and the other response key triggered the playback of a conspecific song different from her colony's song type, which we refer to as the "Non-Colony Song Type" (N-CST). It has been demonstrated that female zebra finches are able to generalise their learnt preference for a specific song (usually the father's song) to the songs of other unfamiliar males

(Clayton, 1990; but see Riebel & Smallegange, 2003). Therefore, and in order to prevent an effect of familiarity in our experiment, both song types used as stimuli were produced by unfamiliar birds. As males from colony A1 and A2 sung the same song type, the CST for A1 females were songs taken from males of colony A2 and vice versa. Males of colony B singing a different song type, the CST for females of colony B were songs of different males that had been trained to produce a good imitation of the song model B but that were not used as founder males for this colony. N-CST for females of the three colonies were sung by males originating from the general pool of zebra finches of the Max Planck Institute for Ornithology in Seewiesen (Germany). Spectrographic illustrations of the different males' songs that could be used as a N-CST are presented in Figure S1.

a) Song recordings

We used recordings of undirected songs produced by males when alone in the cage as it is easier to get high-quality recordings of undirected songs than directed songs. Recordings of directed songs are often polluted by cage noises due to courtship displays of males and calls produced by females. Female preference for undirected songs produced by different males have already been shown in female zebra finches (e.g. Holveck & Riebel, 2007; Riebel et al., 2002). Recordings were made in sound-proof chambers with a Behringer C-2 microphones and a PreSonus AudioBox (24 bit/96K) recording interface. Before subsequent processing, we applied a high pass filter at 420 Hz (Lachlan et al., 2016) and set the peak amplitude to 90% to all the sound files of each male, using the Goldwave software (v6.36).

b) Selection of songs based on the song model

The zebra finch song is produced in bouts: each song bout usually starts by introductory syllables, followed by one or several renditions of the motif (Figure 1B). Syllables are

vocalisations that are separated from each other by silent gaps, and the motif is defined as a short and stereotyped sequence of syllables (Figure 1B). It is the largest repeated unit in the song produced by a given male. As the motif of a given male can contain syllables that cannot be traced back to the original song model used to train the founders of his colony, we defined another song unit: the "core motif". The core motif of a male corresponds to the largest repeated song unit which can be traced back to the original song model (Figure 1B). Thus, in contrast to the motif, the core motif depends on the song model of the colony and allows a better comparison between the males' songs within a colony. According to the fidelity with which a bird imitated the song model, the core motif can either be identical to the motif, or different. Indeed, in the current study some males produced a motif that was longer than the core motif, because they added one or several syllables before or after the core motif (Figure 1B). To select song stimuli that best represented the colony's song type, we chose only songs from males that produced a very good copy of the song model. To do so, we quantified a similarity score between the core motif of the male and the song model of his colony, using the song similarity procedure of SAP 2011 (Tchernichovski et al., 2000; see chapter I of this thesis). Males whose songs were chosen as CST stimuli had a high similarity to the song model (mean ± SD = 87 ± 8).

c) Creation of song stimuli

After selecting the best males for the CST, we created the final song stimuli. To do so, we first selected several song files per male which had a song that could serve as a CST or a N-CST in one of the three colonies. Then, for each male, we selected one natural song bout and digitally modified it using Avisoft SASLab Pro. The aim was to obtain song stimuli that were of similar duration and to mimic the high acoustic stereotypy of natural directed songs (Sossinka & Böhner, 1980). Thus, in the song bout of each male, we kept the three last introductory

syllables (preceding the first motif), followed by four renditions of the motif. Depending on the male, we kept either the first song motif that was then copied three times, or the first two song motifs that were then copied once. We removed potential syllables occurring between the motifs ("connectors", see Hyland Bruno & Tchernichovski, 2017). We made sure to keep the natural gap duration between each song motif. To standardize all song stimuli, amplitude was root-mean square equalised with Praat software (peak digitally scaled to 0.99).

To avoid pseudoreplication, we created 10 unique song sets, each song set being composed of four songs produced by four different males: 1) one male producing a N-CST (conspecific song), 2) one male from colony A2 producing a CST for colony A1 females, 3) one male from colony A1 producing a CST for colony A2 females, 4) one male originally trained to sing the song model B, producing a CST for colony B females (Figure 1B). Among the ten song sets, only seven contained a CST for females of colony B. Indeed, we did not have enough males singing a good copy of the song model B. Therefore, in colony A1 and A2, we assigned a specific song set between 1 and 10 to each female, whereas in colony B, we assigned to each female a song set between 1 and 7. The same N-CST was broadcasted to females from different colonies who were given the same song set. However, depending on the colony of the female, the CST broadcasted was not the same (Table S1). Within one song set, we matched song duration as much as possible (Table S1). The mean duration of songs (± SD) was: N-CST songs = 4.09 ± 1.10 s; CST songs for females of colony A1 = 3.75 ± 0.99 s; CST songs for females of colony A2 = 3.73 ± 1.14 s; CST songs for females of colony B = 3.37 ± 0.47 s. Within each colony, several females could be tested with the same song set (Table S2).

4) Preference test

Each female subject was taken from her colony and put in the apparatus at around 5 pm (day 0 of the experiment). From this moment on, the female had access to the two response

keys and could hear the two different song types (N-CST and CST) sung by two unfamiliar males, each one being triggered by one of the response keys. The females had permanent access to the keys, but pecking the keys elicited songs only during the day: from 8 am when the lights switched on, to 10 pm when the lights switched off. As females had to learn how to peck the keys, the first experimental session started with a trial period of two days (day 1 and day 2 of the experiment). A female could learn to peck the keys by autoshaping after she accidentally pecked a key. We considered that a female had successfully learned to peck the key if we detected at least 10 pecks on each key in one day (first learning criterion). The day this success criterion was reached was considered day 1 of the preference test. Following day 1 of the preference test, we let the female interact freely with the keys during the three following days (day 2, 3 and 4 of the preference test), before putting her back in her colony. Thereby, the preference test lasted four full days with a reversal of both stimuli each night, to control for side preferences: two days with the CST triggered by the right key, and two days with the CST triggered by the left key. Females that had not started to regularly peck the keys at the end of the trial period (morning of day 3 of the experiment) underwent a training procedure.

The training period lasted a maximum of five days (from day 3 to day 7 of the experimental session) and consisted of two daily reinforcement sessions. Reinforcement was provided by 1) drawing the attention of the female to the keys by manually pushing each key several times when she was watching, and 2) sticking seeds or nesting material to the response keys to enhance the appeal of the keys. We kept tracking the pecks realised by the female after each reinforcement session. If the female still had not started to regularly peck the keys at the end of the five-days training period (day 7 of the experiment), she was transferred back to her colony where she rested for at least a week before a second identical experimental session started. Some females exhibited a side preference that could not be overturned by temporarily hiding the preferred key and reinforcing the non-preferred key during the training period. For

those females, we considered that they learned how to peck a key if they pecked the preferred key at least 20 times a day (second learning criterion). If a female failed to reach one of the two learning criteria during the second experimental session, she underwent a third experimental session after at least a week of rest spent in her colony.

If during one of the training sessions, the female started to regularly peck on both, or on one particular key, training was stopped. The day that the female reached one of the two learning criteria without any reinforcement was considered day 1 of her preference test. From day 1, the test continued until day 4. Some females did not learn to press the keys during the first three experimental sessions. Those females were put in the apparatus for a fourth experimental session, this time without any training, giving them a last opportunity to spontaneously learn to peck the keys. If females still had not succeed to reach one of the two learning criteria at the end of this fourth experimental session, we considered that they failed the experiment.

The procedure of the whole experiment is presented in Figure 2B. At any moment of the experiment, we could check whether the female intentionally pecked the keys using webcams that were running continuously during the day.

5) Ethical note

All procedures reported in this paper followed the European regulations on animal experimentation and were approved by the French Ministry for National Education, Higher Education and Research (authorization no. 02609.02). This study was designed to minimize disturbance, stress, and social isolation. No birds were sacrificed for this study.

6) Analysis

Females used several techniques to press the keys, such as pecking it with the beak, pushing it with the feet or the wing, jumping on it or pushing the key by quickly turning around while standing very close to it. For the sake of simplicity, we refer to all these techniques as "pecking" throughout the article. Due to webcam issues, for three females (one in colony A1 and two in colony B), we had no video confirmation of their pecking success. However, those females had pecked both keys a significant number of times, which led us to believe that those pecks were intentional.

Forty one out of 63 tested females succeeded to reach one of the two learning criteria. One of them died at the end of her third day of preference test, and three females pecked the keys less than 20 times on the second day of test. Those four females were thus excluded from the analysis. That left us with a total of 37 females for further analysis (colony A1: n = 10; colony A2: n = 11; colony B: n = 16). Within these females, 17 expressed a side preference and pecked almost exclusively on one of the two response keys: 6 females in colony A1, 3 in colony A2 and 8 in colony B. These females pecked the less preferred key less than 10 times a day (mean number of pecks per day ± SD = 1 ± 2). In the preference analysis of these females, we only focused on pecks on the preferred key, to test whether they pecked more on the preferred key when it was triggering the CST or the N-CST.

Fifteen out of 37 females succeeded to pass the preference test during the first experimental session (colony A1: n = 3; colony A2: n = 5; colony B: n = 7), 3 during the second experimental session (colony A2: n = 1; colony B: n = 2), 4 during the third experimental session (colony A1: n = 3; colony B: n = 1), and 15 during the fourth (colony A1: n = 4; colony A2: n = 5; colony B: n = 6) (Table S3). For the number of successful females tested with each song set, see Table S2.

To analyse the females' preferences, we calculated their preference ratio for the CST: total number of pecks for the CST during the four days of test, divided by the grand total of pecks over the four days period.

7) Statistical analysis

To assess the individual preference of all females (N = 37) for the CST or the N-CST, we performed one binomial test per female (function *binom.test* in R), in order to test whether the preference ratio for the CST significantly differed from 0.5 (chance level). We controlled for multiple testing by correcting all 37 individual *p*-values with the *p.adjust* function in R, using the false discovery rate correction (Benjamini & Hochberg, 1995). To investigate whether there was a significant preference for the CST at the group level in each colony, we checked whether the mean preference ratio was greater than chance by comparing it to 0.5 using a one-sample t-test.

Finally, we tested whether the behavioural responses during the preference test differed between the three colonies to check whether there was a higher preference ratio for the CST or a higher number of pecks during the test in one of the three colonies. We ran two separate generalized mixed models (GLMMs), one for each of our response variables. The first model tested whether the preference ratio for the CST differed according to the colony and the second model tested whether the total number of pecks differed between colonies. Both models included as a fixed effect, the number of experimental sessions that the female needed to reach either of the two learning criteria (i.e. whether she was successful in the 1st, 2nd, 3rd or 4th experimental session). This variable is later referred to as "sessions to success". Both models also included the number (ID) of the song set the female was tested with, as a random effect. Before running the GLMMs, we checked that there was no collinearity between the two variables "colony" and "sessions to success". We checked for overdispersion and because we

detected overdispersion in both models, we used error distributions from the quasi family. To test the preference ratio for the CST, we used a GLMM with a quasibinomial distribution and a logit link function. For each female (N = 37), the response variable was weighted by the total number of pecks she made during the four days of test (using the *weights* parameter). For the total number of pecks, we used a GLMM with a quasipoisson distribution and a log link function. Both models were performed using the *glmmPQL* function from the *MASS* package in R. The levels of each explanatory factor (i.e. "colony" and "sessions to success ") were compared to each other by computing post-hoc Tukey tests with the *emmean*s package in R (Lenth, 2018).

RESULTS

In the three colonies, most females significantly preferred one of the two song types, i.e. their preference ratio (number of pecks for the CST/total number of pecks) was significantly different from 0.5 (Figure 3, Table 1 & Table S3). Additionally, the majority of those females preferred the CST over the N-CST (Figure 3, Table 1 & Table S3).

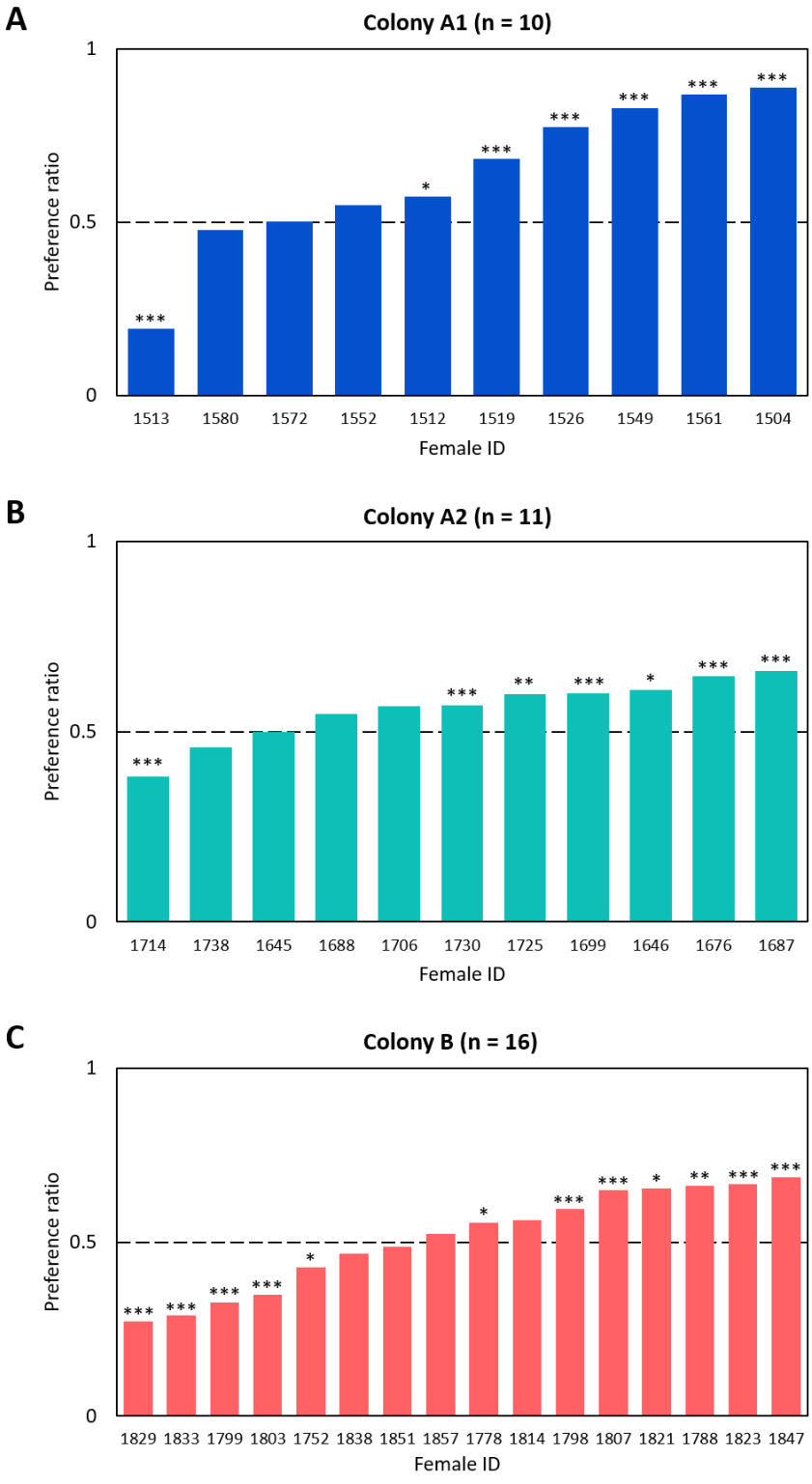

Figure 3. Preference ratios (pecks for the Colony Song Type (CST)/total number of pecks) for each female of: (A) colony A1, (B) colony A2, and (C) colony B. Preference ratios approaching 1 indicate a preference for the CST, preference ratios approaching 0 indicate a preference for the Non-Colony Song Type (N-CST). Asterisks (*) indicate a significant preference for one of the two song types (see Table 1 & Table S3).

Table 1. Number and percentage of tested females in each colony that exhibited no preference, or a significant preference for the Colony Song type (CST) or for the Non-Colony Song Type (N-CST). In each colony, most females showed a preference for the CST.

Colony	n		Females with no preference	Females with a preference		
				For the CST	For the N-CST	Total
A1	10	*n*	3	6	1	7
		%	30	60	10	70
A2	11	*n*	4	6	1	7
		%	36	55	9	64
B	16	*n*	4	7	5	12
		%	25	44	31	75

However, this preference for the colony song type was not reflected at the group level in all colonies. Indeed, the preference for the CST was only significant in colony A2 (tested as a deviation from a 0.5 preference ratio with one-sample t-test: t = 2.30, df = 10, $p = 0.044$; Figure 4). In colony A1 and B, the mean preference ratio was not significantly different from the chance level of 0.5 (colony A1: t = 1.94, df = 9, $p = 0.084$; colony B: t = 0.31, df = 15, $p = 0.762$; Figure 4).

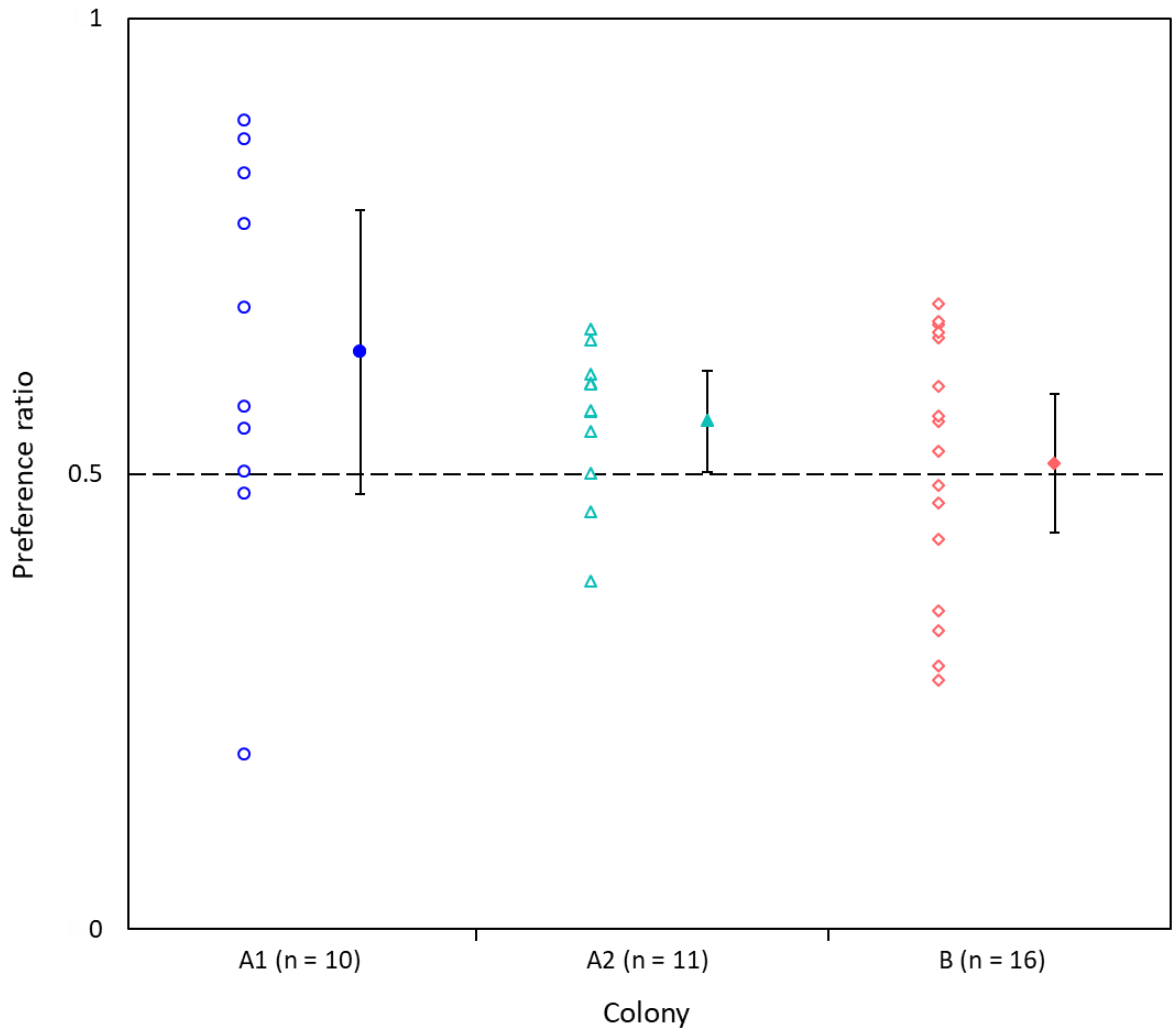

Figure 4. Preference ratio for the Colony Song Type (CST) over the Non-Colony Song Type (N-CST) in each colony. Blank symbols represent individual females' preference ratios. Filled symbols represent the mean preference ratio (with 95% confidence interval). Preference ratios approaching 1 indicate a preference for the CST, preference ratios approaching 0 indicate a preference for the N-CST. The mean preference ratio was only significantly different from a 0.5 preference ratio (dashed line) in colony A2 (one sample t-test, $p = 0.044$).

The absolute number of key pecks over the four days of test varied highly between females (Table S3). In order to investigate a possible link between motivation and preference, we tested whether females that pecked more also had stronger preferences. We measured preference strength as the number of pecks for the preferred song type, divided by the number

of pecks for the less preferred song type. There was no significant correlation between the total number of key pecks and preference strength in any of the colonies (Spearman's *r*, all *ns*).

We then further investigated the differences between colonies in the two main responses: preference ratio and total number of key pecks. We found that the preference ratio for the CST in colony A1 was higher than in colony B (Table 2). No difference in the preference ratio was found between the colonies A1 and A2, as well as between colony A2 and colony B (Table 2). As females differed in the number of experimental sessions needed to successfully learn how to peck the keys (Table S3), we also tested whether this factor ("sessions to success") influenced the two main behavioural responses. The number of experimental sessions needed to reach either of the two learning criteria did not have any effect on the preference ratio (all pairwise comparisons were *ns*, see Table 2). Two colonies differed in their activity levels: we found that females of colony A1 significantly pecked more often the keys during the test than females of colony B (Table 2). However, there was no significant difference in the total number of pecks between colony A1 and A2 or between A2 and B (Table 2). There was no effect of the number of experimental sessions needed to succeed on the total number of pecks (all pairwise comparisons are *ns*, see Table 2).

Table 2. Tukey post-hoc pairwise comparisons for the two GLMMs on the preference ratio for the Colony Song Type (CST) and on the total number of key pecks during the four days of preference test. Colony and number of experimental sessions needed to reach either of the two learning criteria ("sessions to success") are fixed factors. Significant differences are in bold. df = 22.

Source of variation	Pairwise comparison	Preference ratio				Total number of key pecks			
		Estimate	SE	*t*	*p*	Estimate	SE	*t*	*p*
Colony	A1 - A2	0.462	0.301	1.534	0.295	1.032	0.518	1.993	0.138
	A1 - B	**0.657**	**0.239**	**2.753**	**0.03**	**1.423**	**0.528**	**2.693**	**0.034**
	A2 - B	0.195	0.195	0.64	0.799	0.391	0.54	0.725	0.752
Sessions to success	1 - 2	-0.0387	0.345	-0.112	0.999	-1.412	0.636	-2.221	0.149
	1 - 3	-0.4767	0.416	-1.145	0.666	0.575	0.781	0.737	0.881
	1 - 4	0.0229	0.232	0.099	0.99	-0.244	0.462	-0.527	0.951
	2 - 3	-0.4381	0.506	-0.865	0.822	1.987	0.921	2.157	0.167
	2 - 4	0.0616	0.349	0.176	0.998	1.168	0.662	1.879	0.265
	3 - 4	0.4996	0.403	1.239	0.61	-0.819	0.747	-1.097	0.695

DISCUSSION

In this study, the majority of female zebra finches exhibited a clear preference for the Colony Song Type (CST) over the Non-Colony Song Type (N-CST), regardless of their native colony. Yet, this preference for the songs that resemble those produced by males of their colony was not reflected at the group level in all three colonies. Additionally, these individual preferences were not due to the level of motivation of the female. The preference for the CST as well as the activity levels of females appeared to be stronger in the first colony (A1) than in the third colony (B), but both were not affected by the number of experimental sessions females needed to reach either of the two learning criteria (10 pecks on each key, or 20 pecks on one of the two keys on a same day).

Our results are in line with several previous studies which showed that females of this species prefer the song they experienced during their early life (for a review, see Riebel, 2009). However, the current study differs from those earlier studies that usually gave females a choice between the song of an unfamiliar male and a familiar one, such as the father's song, the tutor's song or a song heard from playback during the sensitive phase of song preference learning (Clayton, 1988; Miller, 1979a; Riebel, 2000; Riebel et al., 2002). The fact that our females still preferred the CST over the N-CST even if it was sung by an unfamiliar individual, suggests that this learned preference was strong enough to be generalised to an unfamiliar emitter. This confirms what has already been found in the zebra finch, namely the females' ability to generalise the learnt song preference to songs of unfamiliar males (Clayton, 1990; Riebel, 2009). Additionally, we found that this preference for the CST did not depend on the colony's song dialect: A or B. Indeed, in all three colonies (colony A1 and A2 singing the song dialect A and colony B singing the song dialect B), most females exhibited a preference for the CST.

Even if some weak geographical variations in the song had been described in Australian populations of zebra finches (Zann, 1993), the salience of theses variations to females have not been studied so far. By creating artificially dialects in the laboratory, we were able to show here that these acoustic variations matter to female zebra finches. In other species, the significance of local song dialects to females has been investigated in the context of mate choice. For example, female Nuttall's white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) were more stimulated by male song of their natal dialect than adjacent dialects (Baker, 1983). Furthermore, it has been argued that female preferences play an important role in the stability of song dialects (reviews in Payne et al., 1981; Baker & Cunningham, 1985; Rothstein & Fleischer, 1987). In the brown-headed cowbird (*Molothrus ater*) females show sexual preferences for the correct local whistle type, which could create a selection pressure on males to conform to the local song type and result in influencing the dialects' stability (O'Loghlen & Rothstein, 1995, 2003). The

brown-headed cowbird is an interesting case as this is a brood parasitic species in which young birds are not exposed to conspecific song during their early life. Several studies proposed that male song learning may likewise be influenced by females in the zebra finch. For instance, the song imitation of an adult male is better when a hearing female is housed with the learning pupil (Adret, 2004) and worse when housed with a deaf female (Williams, 2004). More recently, another study suggested that the process of song learning in young males could be guided by the social feedback of an adult female zebra finch (Carouso-Peck & Goldstein, 2019). In this context, and together with the knowledge that females prefer songs that are consistent to their home dialect, we could think that female preferences had a determining role in the establishment and stability of song dialects in our artificial colonies of zebra finches. That is, females' preference for the CST (very similar to the original song model), might have guided young males to conform to this song model.

Unlike most zebra finch female preference studies in which tested females were housed in single-sex groups with no contact of any sort with males prior to the preference test (Holveck & Riebel, 2007; Riebel 2000; Riebel et al., 2002), females in the current study spent their whole life with males with whom they could interact freely. We could therefore hypothesise that their exhibited preferences were weaker than if they had been housed separately from males. However, those conditions also allowed females to breed freely with males of their colony during the course of the communal breeding, unlike most studies in which tested females never had any breeding experience (Holveck & Riebel, 2007, 2010; Riebel, 2000; Riebel et al., 2002). We did not check whether a specific female already had breeding experience and if she had a mate at the time she was tested, which could have had an impact on individual female preferences. Mated female zebra finches express a significant preference for their mate's song over an unfamiliar one (Miller, 1979b). Thus, we could hypothesise that females who did not show a clear preference for the CST were paired to males producing a poor version of this song

type. Indeed, in the three colonies, even if most males conformed to the colony's song type, some males produced songs that deviated from it (Derégnaucourt et al., 2014; see chapter I of this thesis). It is possible that some females were paired to such males and had participated to the breeding of their colony prior to the preference test.

Despite the individual preferences of females for the CST, this preference was not reflected at the group level in all three colonies. Moreover, some females exhibited significant preferences for the N-CST. In other species such as canaries (*Serinus canaria*), females exhibit clear preferences for particular song syllables (Vallet & Kreutzer, 1995). However, there is no convincing evidence so far that female zebra finches exhibit preferences for particular sounds in male songs. Nevertheless, we cannot exclude that some females in the current study preferred particular sound characteristics of certain N-CST stimuli.

Since some females did not succeed to learn how to peck the keys during the first experimental session, we could have expected an effect of the number of experimental sessions needed to reach either one of the two learning criteria on the preference for the CST and the activity level of females. This was not the case, suggesting that the rapidity with which a female learned the operant task was not related to her preference strength or her motivation to peck the keys. However, we did find some differences between the colonies in the preference ratio for the CST and in the activity levels of females during the test. Females of colony A1 exhibited a higher preference ratio for the CST and a higher number of pecks than females of colony B. The nature of the song dialect (A or B) cannot explain this finding, as no differences were found between colony A2 and B. It has been reported that females' experience during adulthood could influence song preferences; for example in canaries (Béguin et al., 1998; Nagle & Kreutzer, 1997), but also in zebra finches, in which females can develop preferences as adults (Clayton, 1988; Miller, 1979b; Riebel, 2009). Thus, we could assume that our females' adult experience

with song affected their preference strength. Given that our females were housed with males during their whole lives, we propose that the experience with the song type of males and the ability for females to interact with them reinforced the previously learned preference. When tested, females of colony A1 were much older than females of colony B. Therefore, they had more experience with the CST, which could have resulted in a stronger preference for the CST and a higher motivation to hear it.

Over the years, operant conditioning has been established as an effective paradigm to test females' preferences in zebra finches, because they can express their preferences through an active choice (e.g. Holveck & Riebel, 2007; Honarmand et al., 2015; Houx & ten Cate, 1999; Riebel, 2000; Riebel et al., 2002). However, other methods can also be used, such as phonotaxis in response to male songs or even live males (Forstmeier & Birkhead, 2004; Holveck & Riebel, 2007). Unlike song, calls are vocalisations frequently emitted by zebra finches of both sexes. Calls are produced by members of a mated pair when visually isolated (Zann, 1996) and used for mate recognition (Vignal et al., 2004, 2008) or for regulating social interactions within the groups (Elie et al., 2011). Because calls are meaningful vocalisations, measuring the number of calls produced by females during song broadcast could be another way of assessing female preferences in zebra finches. Such an approach has already been successfully used in other species (genus Coturnix, quails: Derégnaucourt & Guyomarc'h, 2003; Domestic canary: Amy et al., 2015; Nagle et al., 2002; Salvin et al., 2018). Furthermore, in zebra finches, it has already been demonstrated that call rate was an indicator of song discrimination (Clayton, 1988). If the colony's dialect is important to female zebra finches in a sexual and/or social context, their preference for this song type should be consistent using these various methods and should also be repeatable over time (Holveck & Riebel, 2007).

In zebra finches, the lack of seasonality in breeding (Immelmann, 1962; Zann, 1996) raises some issues concerning the nature of the observed preferences in females. Indeed, in our study we did not test for female sexual receptivity. Therefore, we may wonder whether the expressed preference for the CST is a sexual preference related to mate choice, or a social preference. In social species, shared song types favour group cohesion (Hausberger et al., 2008). Accordingly, song could be interpreted as an affiliative signal rather than a mere sexual signal in such species. Such social preferences could have played a role in our study as well. To assess this possibility, a social learning task could be used. In zebra finches, the classical observer-demonstrator paradigm has been proven effective to assess social learning in a context of food choice (Benskin et al., 2002; Guillette & Healy, 2014; Katz & Lachlan, 2003; Riebel et al., 2012). Therefore, if song dialects do constitute a social marker, an observer should preferentially learn his food choice from a bird singing the CST than from a bird singing the N-CST. Female as well as male zebra finches should be tested as observers to determine whether song dialects could constitute an affiliative signal in this species.

In conclusion, our work expands on numerous studies showing that zebra finch females express a preference for the song they heard early in life but is the first to demonstrate a direct link between song dialects and female preference in this species. Our findings also underline the difficulty of concluding on whether expressed female preferences in zebra finches are more related to a social or to a sexual preference, but they pave the way to check whether song dialects can be used as an affiliative signal in the context of social learning in this model species.

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REFERENCES

Adret, P. (2004). Vocal imitation in blindfolded zebra finches (*Taeniopygia guttata*) is facilitated in the presence of a non-singing conspecific female. *Journal of Ethology*, *22*(1), 29–35. https://doi.org/10.1007/s10164-003-0094-y

Amy, M., Salvin, P., Naguib, M., & Leboucher, G. (2015). Female signalling to male song in the domestic canary, *Serinus canaria*. *Royal Society Open Science*, *2*(1), 140196. https://doi.org/10.1098/rsos.140196

Andersson, M. B. (1994). *Sexual Selection*. Princeton University Press.

Baker, M. C. (1983). The behavioral response of female Nuttall's White-crowned Sparrows to male song of natal and alien dialects. *Behavioral Ecology and Sociobiology*, *12*(4), 309–315. https://doi.org/10.1007/BF00302898

Baker, M. C., & Cunningham, M. A. (1985). The Biology of Bird-Song Dialects. *Behavioral and Brain Sciences*, *8*(1), 85–100. https://doi.org/10.1017/S0140525X00019750

Beecher, M. D., Campbell, S. E., & Nordby, J. C. (2000). Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal Behaviour*, *59*(1), 29–37. https://doi.org/10.1006/anbe.1999.1304

Béguin, N., Leboucher, G., & Kreutzer, M. L. (1998). Sexual Preferences for Mate Song in Female Canaries (*Serinus Canaria*). *Behaviour*, *135*(8), 1185–1196. https://doi.org/10.1163/156853998792913500

Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, *57*(1), 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Benskin, C. M. H., Mann, N. I., Lachlan, R. F., & Slater, P. J. B. (2002). Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, *64*(5), 823–828.

https://doi.org/10.1006/anbe.2002.2005

Briefer, E., Aubin, T., Lehongre, K., & Rybak, F. (2008). How to identify dear enemies: The group signature in the complex song of the skylark *Alauda arvensis*. *Journal of Experimental Biology*, *211*(3), 317–326. https://doi.org/10.1242/jeb.013359

Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews*, *78*(4), 575–595.

Carouso-Peck, S., & Goldstein, M. H. (2019). Female Social Feedback Reveals Non-imitative Mechanisms of Vocal Learning in Zebra Finches. *Current Biology*. https://doi.org/10.1016/j.cub.2018.12.026

Catchpole, C. K., & Slater, P. J. B. (2008). Bird Song: Biological Themes and Variations. *Cambridge University, Cambridge*.

Clayton, N. S. (1988). Song discrimination learning in zebra finches. *Animal Behaviour*, *36*(4), 1016–1024. https://doi.org/10.1016/S0003-3472(88)80061-7

Clayton, N. S. (1990). Subspecies recognition and song learning in zebra finches. *Animal Behaviour*, *40*(6), 1009–1017. https://doi.org/10.1016/S0003-3472(05)80169-1

Cynx, J., & Nottebohm, F. (1992). Role of gender, season, and familiarity in discrimination of conspecific song by zebra finches (*Taeniopygia guttata*). *Proceedings of the National Academy of Sciences*, *89*(4), 1368–1371.

Derégnaucourt, S., & Guyomarc'h, J. C. (2003). Mating Call Discrimination in Female European (*Coturnix c. Coturnix*) and Japanese Quail (*Coturnix c. Japonica*). *Ethology*, *109*(2), 107–119. https://doi.org/10.1046/j.1439-0310.2003.00854.x

Derégnaucourt, S., Nagle, L., Gahr, M., Aubin, T., & Geberzahn, N. (2014). Cultural Evolution of Birdsong in the Laboratory. *Neuroscience Annual Meeting 2014*.

Derryberry, E. P. (2007). Evolution of Bird Song Affects Signal Efficacy: An Experimental Test Using Historical and Current Signals. *Evolution*, *61*(8), 1938–1945. https://doi.org/10.1111/j.1558-5646.2007.00154.x

Elie, J. E., Soula, H. A., Mathevon, N., & Vignal, C. (2011). Dynamics of communal vocalizations in a social songbird, the zebra finch (*Taeniopygia guttata*). *The Journal of the Acoustical Society of America*, *129*(6), 4037–4046. https://doi.org/10.1121/1.3570959

Forstmeier, W., & Birkhead, T. R. (2004). Repeatability of mate choice in the zebra finch: Consistency within and between females. *Animal Behaviour*, *68*(5), 1017–1028.

García, N. C., Arrieta, R. S., Kopuchian, C., & Tubaro, P. L. (2015). Stability and change through time in the dialects of a Neotropical songbird, the Rufous-collared Sparrow. *Emu*, *115*(4), 309–316.

Gil, D., & Gahr, M. (2002). The honesty of bird song: Multiple constraints for multiple traits. *Trends in Ecology & Evolution*, *17*(3), 133–141. https://doi.org/10.1016/S0169-5347(02)02410-2

Guillette, L. M., & Healy, S. D. (2014). Mechanisms of copying behaviour in zebra finches. *Behavioural Processes*, *108*, 177–182. https://doi.org/10.1016/j.beproc.2014.10.011

Harbison, H., Nelson, D. A., & Hahn, T. P. (1999). Long-Term Persistence of Song Dialects in the Mountain White-Crowned Sparrow. *The Condor*, *101*(1), 133–148. https://doi.org/10.2307/1370454

Hausberger, M., Bigot, E., & Clergeau, P. (2008). Dialect use in large assemblies: A study in European starling *Sturnus vulgaris* roosts. *Journal of Avian Biology*, *39*(6), 672–682.

Holveck, M. J., & Riebel, K. (2007). Preferred songs predict preferred males: Consistency and repeatability of zebra finch females across three test contexts. *Animal Behaviour*, *74*(2), 297–309.

Holveck, M. J., & Riebel, K. (2010). Low-quality females prefer low-quality males when choosing a mate. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1678), 153–160. https://doi.org/10.1098/rspb.2009.1222

Honarmand, M., Riebel, K., & Naguib, M. (2015). Nutrition and peer group composition in early adolescence: Impacts on male song and female preference in zebra finches. *Animal Behaviour*, *107*, 147–158. https://doi.org/10.1016/j.anbehav.2015.06.017

Houx, A. B., & ten Cate, C. (1999). Song learning from playback in zebra finches: Is there an effect of operant contingency? *Animal Behaviour*, *57*(4), 837–845. https://doi.org/10.1006/anbe.1998.1046

Hyland Bruno, J., & Tchernichovski, O. (2017). Regularities in zebra finch song beyond the repeated motif. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2017.11.001

Immelmann, K. (1969). Song development in the zebra finch and other estrildid finches. *Bird*

Vocalizations, *61*.

Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews*, *72*(2), 283–327.

Katz, M., & Lachlan, R. F. (2003). Social learning of food types in zebra finches (*Taenopygia guttata*) is directed by demonstrator sex and feeding activity. *Animal Cognition*, *6*(1), 11–16. https://doi.org/10.1007/s10071-003-0158-y

King, A. P., West, M. J., & Eastzer, D. H. (1980). Song structure and song development as potential contributors to reproductive isolation in cowbirds (*Molothrus ater*). *Journal of Comparative and Physiological Psychology*, *94*(6), 1028–1039. https://doi.org/10.1037/h0077737

Kroodsma, D. E. (1976). Reproductive development in a female songbird: Differential stimulation by quality of male song. *Science*, *192*(4239), 574–575.

Lachlan, R. F., van Heijningen, C. A., ter Haar, S. M., & ten Cate, C. (2016). Zebra Finch Song Phonology and Syntactical Structure across Populations and Continents—A Computational Comparison. *Frontiers in Psychology*, *7*. Retrieved from http://www.ncbi.nlm.nih.gov/pmc/articles/PMC4935685/

Lauay, C., Gerlach, N. M., Adkins-Regan, E., & DeVoogd, T. J. (2004). Female zebra finches require early song exposure to prefer high-quality song as adults. *Animal Behaviour*, *68*(6), 1249–1255. https://doi.org/10.1016/j.anbehav.2003.12.025

Lenth, R. V. (2018). *Estimated Marginal Means, aka Least Squares Means. R Package version 1.1*.

MacDougall-Shackleton, E. A., & MacDougall-Shackleton, S. A. (2001). Cultural and Genetic Evolution in Mountain White-Crowned Sparrows: Song Dialects Are Associated with Population Structure. *Evolution*, *55*(12), 2568–2575. https://doi.org/10.1111/j.0014-3820.2001.tb00769.x

MacDougall-Shackleton, S. A., MacDougall-Shackleton, E. A., & Hahn, T. P. (2001). Physiological and behavioural responses of female mountain white-crowned sparrows to natal-and foreign-dialect songs. *Canadian Journal of Zoology*, *79*(2), 325–333.

Marler, P., & Tamura, M. (1962). Song 'Dialects' in Three Populations of White-Crowned Sparrows. *The Condor*, *64*(5), 368–377. https://doi.org/10.2307/1365545

Marler, P., & Tamura, M. (1964). Culturally transmitted patterns of vocal behavior in sparrows. *Science*, *146*(3650), 1483–1486.

Miller, D. B. (1979a). Long-term recognition of father's song by female zebra finches. *Nature*, *280*, 389–391.

Miller, D. B. (1979b). The acoustic basis of mate recognition by female zebra finches (*Taeniopygia guttata*). *Animal Behaviour*, *27*, 376–380.

Nagle, L., & Kreutzer, M. L. (1997). Adult female domesticated canaries can modify their song preferences. *Canadian Journal of Zoology*, *75*(8), 1346–1350. https://doi.org/10.1139/z97-759

Nagle, Laurent, Kreutzer, M. L., & Vallet, E. (2002). Adult female canaries respond to male song by calling. *Ethology*, *108*(5), 463–472.

Nottebohm, F. (1969). The song of the chingolo, *Zonotrichia capensis*, in Argentina: Description and evaluation of a system of dialects. *The Condor*, *71*(3), 299–315.

Nottebohm, F. (1972). The Origins of Vocal Learning. *The American Naturalist*, *106*(947), 116–140. https://doi.org/10.1086/282756

O'Loghlen, A. L., & Rothstein, S. I. (1995). Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. *Behavioral Ecology and Sociobiology*, *36*(4), 251–259. https://doi.org/10.1007/BF00165834

O'Loghlen, A. L., & Rothstein, S. I. (2003). Female preference for the songs of older males and the maintenance of dialects in brown-headed cowbirds (*Molothrus ater*). *Behavioral Ecology and Sociobiology*, *53*(2), 102–109. https://doi.org/10.1007/s00265-002-0551-6

Payne, R. B. (1981). Population structure and social behaviour: Models for testing the ecological significance of song dialects in birds: *In: Alexander RD & Tinkle DW (eds): Natural selection and social behaviour: Recent Research and New Theory*. Chiron Press. New York: 108.

Payne, R. B. (1982). Ecological Consequences of Song Matching: Breeding Success and Intraspecific Song Mimicry in Indigo Buntings. *Ecology*, *63*(2), 401–411. https://doi.org/10.2307/1938958

Payne, R. B. (1983). The social context of song mimicry: Song-matching dialects in indigo buntings (*Passerina cyanea*). *Animal Behaviour*, *31*(3), 788–805. https://doi.org/10.1016/S0003-

3472(83)80236-X

Payne, R. B., Thompson, W. L., Fiala, K. L., & Sweany, L. L. (1981). Local Song Traditions in Indigo Buntings: Cultural Transmission of Behavior Patterns across Generations. *Behaviour, 77*(4), 199–221.

Podos, J., & Warren, P. S. (2007). The Evolution of Geographic Variation in Birdsong. In *Advances in the Study of Behavior* (Vol. 37, pp. 403–458). https://doi.org/10.1016/S0065-3454(07)37009-5

Riebel, K. (2000). Early exposure leads to repeatable preferences for male song in female zebra finches. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1461), 2553–2558.

Riebel, K. (2003). Developmental influences on auditory perception in female zebra finches—Is there a sensitive phase for song preference learning? *Animal Biology*, *53*(2), 73–87. https://doi.org/10.1163/157075603769700304

Riebel, K. (2009). Song and female mate choice in zebra finches: A review. *Advances in the Study of Behavior*, *40*, 197–238.

Riebel, K., & Slater, P. J. B. (1998). Testing female chaffinch song preferences by operant conditioning. *Animal Behaviour*, *56*(6), 1443–1453.

Riebel, K., & Smallegange, I. M. (2003). Does Zebra finch (*Taeniopygia guttata*) preference for the (familiar) father's song generalize to the songs of unfamiliar brothers? *Journal of Comparative Psychology*, *117*(1), 61–66. https://doi.org/10.1037/0735-7036.117.1.61

Riebel, K., Smallegange, I. M., Terpstra, N. J., & Bolhuis, J. J. (2002). Sexual equality in zebra finch song preference: Evidence for a dissociation between song recognition and production learning. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1492), 729–733. https://doi.org/10.1098/rspb.2001.1930

Riebel, K., Spierings, M. J., Holveck, M. J., & Verhulst, S. (2012). Phenotypic plasticity of avian social-learning strategies. *Animal Behaviour*, *84*(6), 1533–1539. https://doi.org/10.1016/j.anbehav.2012.09.029

Ritschard, M., Riebel, K., & Brumm, H. (2010). Female zebra finches prefer high-amplitude song. *Animal Behaviour*, *79*(4), 877–883. https://doi.org/10.1016/j.anbehav.2009.12.038

Rothstein, S. I., & Fleischer, R. C. (1987). Vocal Dialects and Their Possible Relation to Honest Status Signalling in the Brown-Headed Cowbird. *The Condor*, *89*(1), 1–23. https://doi.org/10.2307/1368756

Salvin, P., Derégnaucourt, S., Leboucher, G., & Amy, M. (2018). Consistency of female preference for male song in the domestic canary using two measures: Operant conditioning and vocal response. *Behavioural Processes*, *157*, 238–243. https://doi.org/10.1016/j.beproc.2018.10.004

Searcy, W. A. (1992). Song Repertoire and Mate Choice in Birds. *Integrative and Comparative Biology*, *32*(1), 71–80. https://doi.org/10.1093/icb/32.1.71

Searcy, W. A., & Andersson, M. (1986). Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, *17*(1), 507–533.

Searcy, W.A. & Yasukawa, K. (1996). Song and female choice. *In: Kroodsma, D.E., Miller, E.H. (Eds.), Ecology and Evolution of Acoustic Communication in Birds. Comstock Publishing Associates, Ithaca*, pp. 454–473.

Slater, P. J. B., Eales, L. A., & Clayton, N. S. (1988). Song Learning in Zebra Finches (*Taeniopygia guttata):* Progress and Prospects. *Advances in the Study of Behavior*, *18*, 1.

Sossinka, R., & Böhner, J. (1980). Song types in the zebra finch *Poephila guttata castanotis*. *Zeitschrift Für Tierpsychologie*, *53*(2), 123–132.

Tchernichovski, O., Nottebohm, F., Ho, C. E., Pesaran, B., & Mitra, P. P. (2000). A procedure for an automated measurement of song similarity. *Animal Behaviour*, *59*(6), 1167–1176. https://doi.org/10.1006/anbe.1999.1416

Trainer, J. M. (1983). Changes in Song Dialect Distributions and Microgeographic Variation in Song of White-Crowned Sparrows (*Zonotrichia leucophrys nuttalli*). *The Auk*, *100*(3), 568–582. https://doi.org/10.1093/auk/100.3.568

Vallet, E., & Kreutzer, M. L. (1995). Female canaries are sexually responsive to special song phrases. *Animal Behaviour*, *49*(6), 1603–1610. https://doi.org/10.1016/0003-3472(95)90082-9

Vignal, C., Mathevon, N., & Mottin, S. (2004). Audience drives male songbird response to partner's voice. *Nature*, *430*(6998), 448–451.

Vignal, C., Mathevon, N., & Mottin, S. (2008). Mate recognition by female zebra finch: Analysis of individuality in male call and first investigations on female decoding process. *Behavioural Processes*, *77*(2), 191–198. https://doi.org/10.1016/j.beproc.2007.09.003

Wasserman, F. E., & Cigliano, J. A. (1991). Song output and stimulation of the female in white-throated sparrows. *Behavioral Ecology and Sociobiology*, *29*(1), 55–59. https://doi.org/10.1007/BF00164295

Widemo, F., & Saether, S. A. (1999). Beauty is in the eye of the beholder: Causes and consequences of variation in mating preferences. *Trends in Ecology & Evolution*, *14*(1), 26–31.

Williams, H. (2004). Birdsong and singing behavior. *ANNALS-NEW YORK ACADEMY OF SCIENCES*, 1–30.

Zahavi, A. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, *53*(1), 205–214.

Zann, R. A. (1993). Variation in song structure within and among populations of Australian zebra finches. *The Auk*, 716–726.

Zann, R. A. (1996). *The zebra finch: A synthesis of field and laboratory studies* (Vol. 5). Oxford University Press.

Zollinger, S. A., Goller, F., & Brumm, H. (2011). Metabolic and Respiratory Costs of Increasing Song Amplitude in Zebra Finches. *PLOS ONE*, *6*(9), e23198. https://doi.org/10.1371/journal.pone.0023198

SUPPLEMENTARY MATERIAL

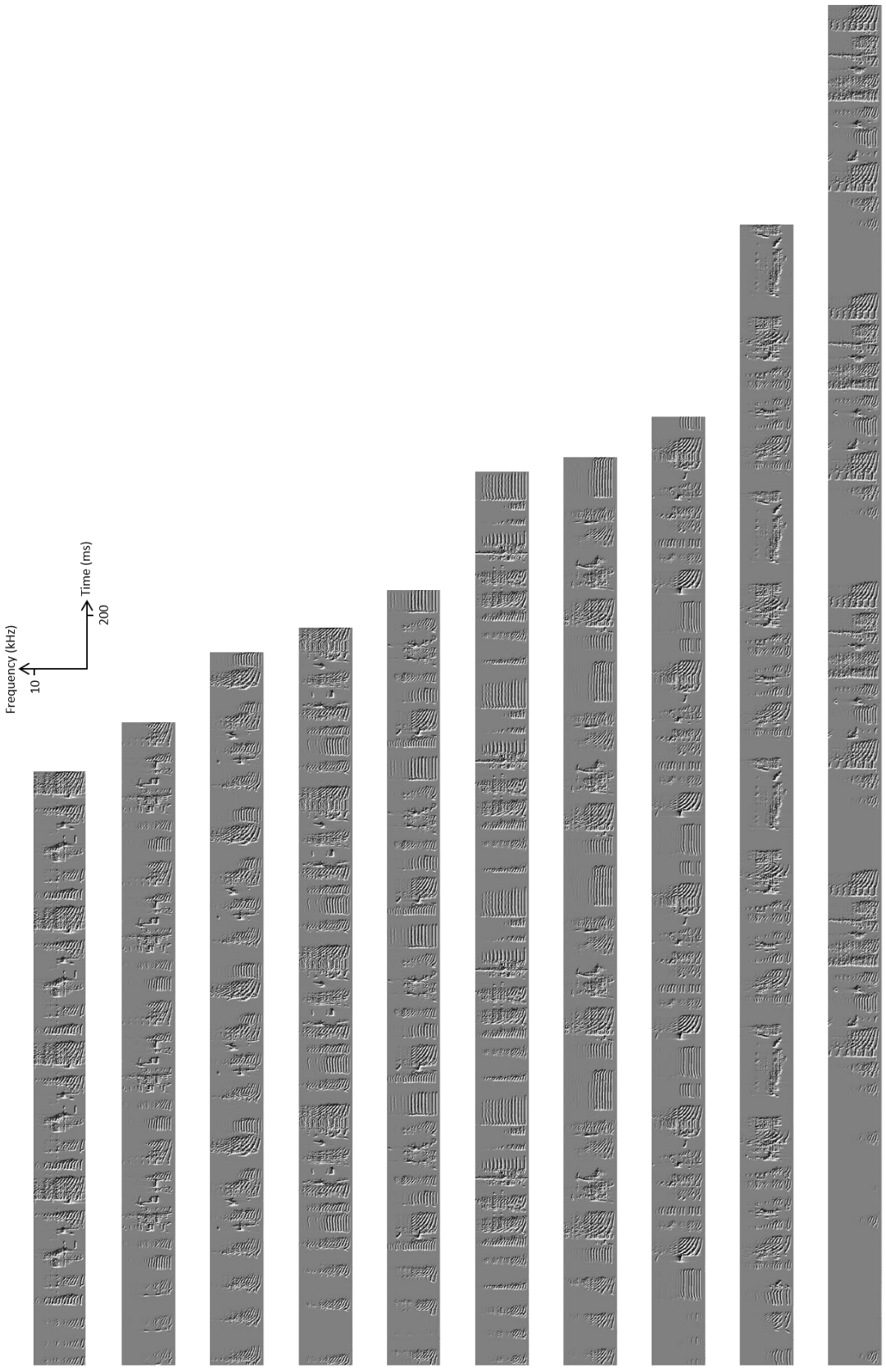

Figure S1. Spectrograms of songs used as a Non-Colony Song Type (N-CST) stimulus. There was a different N-CST stimulus in each song set (a song set was composed of one N-CST stimulus and three Colony Song Type (CST) stimuli; one for females of each colony). The 10 N-CST stimuli came from 10 different adult males originating from the general pool of zebra finches at the Max Planck Institute for Ornithology in Seewiesen (Germany).

Table S1. Duration (s) and singer ID of each song composing the 10 song sets.

Set	Song duration (s)			
	N-CST	CST for colony A1 females	CST for colony A2 females	CST for colony B females
1	2.79	2.62	3.12	2.49
2	3.03	2.82	2.98	3.19
3	3.34	2.72	2.71	3.35
4	3.47	3.41	3.52	3.44
5	3.64	3.37	3.46	3.53
6	4.20	2.88	3.12	3.59
7	4.27	3.95	4.08	4.03
8	4.45	4.34	3.94	-
9	5.36	5.22	4.39	-
10	6.39	5.97	6.12	-
Set	Singer ID			
	N-CST	CST for colony A1 females	CST for colony A2 females	CST for colony B females
1	1	1508	1741	1631
2	290	1559	1670	1643
3	1103	1505	1668	1593
4	13	1506	1737	1720
5	466	1497	1654	1722
6	325	1499	1705	1680
7	406	1569	1728	1615
8	559	1547	1739	-
9	1075	1567	1694	-
10	63	1553	1709	-

Table S2. Number of tested and successful females for each song set.

Set	Number of tested females			Number of successful females		
	Colony A1	Colony A2	Colony B	Colony A1	Colony A2	Colony B
1	2	2	4	2	1	1
2	1	2	4	1	1	3
3	1	2	5	1	2	3
4	1	2	5	1	1	3
5	1	3	5	1	2	3
6	1	3	4	1	0	1
7	1	2	4	1	1	2
8	1	2	-	1	1	-
9	1	1	-	0	1	-
10	1	2	-	1	1	-
Total	n = 11	n = 21	n = 31	n = 10	n = 11	n = 16

Table S3. Information on the preference test for each tested female of the three colonies.

Preference ratios significantly different from 0.5 (chance level) are in bold.

Colony	Female ID	Sessions to success	Number of pecks for CST	Total number of pecks	Preference ratio	*p*-value of binomial test
A1	1504	1	776	874	**0.89**	**< 0.001**
	1512	3	195	340	**0.57**	**0.008**
	1513	4	56	291	**0.19**	**< 0.001**
	1519	1	2055	3012	**0.68**	**< 0.001**
	1526	4	2337	3020	**0.77**	**< 0.001**
	1549	3	272	328	**0.83**	**< 0.001**
	1552	4	206	375	0.55	0.063
	1561	3	998	1150	**0.87**	**< 0.001**
	1572	1	127	253	0.50	1
	1580	4	976	2041	0.48	0.051
A2	1645	1	62	124	0.50	1
	1646	4	101	166	**0.61**	**0.006**
	1676	1	104	161	**0.65**	**< 0.001**
	1687	4	108	164	**0.66**	**< 0.001**
	1688	4	125	229	0.55	0.186
	1699	1	495	826	**0.60**	**< 0.001**
	1706	4	241	425	0.57	0.59
	1714	1	144	377	**0.38**	**< 0.001**
	1725	1	186	311	**0.60**	**< 0.001**
	1730	2	2030	3566	**0.57**	**< 0.001**
	1738	4	108	236	0.46	0.216
B	1752	3	153	358	**0.43**	**0.007**
	1778	1	244	438	**0.56**	**0.019**
	1788	4	53	80	**0.66**	**0.005**
	1798	4	1656	2779	**0.60**	**< 0.001**
	1799	1	142	434	**0.33**	**< 0.001**
	1803	1	84	241	**0.35**	**< 0.001**
	1807	4	133	205	**0.65**	**< 0.001**
	1814	1	72	128	0.56	0.185
	1821	1	38	58	**0.66**	**0.025**
	1823	4	174	261	**0.67**	**< 0.001**
	1829	1	72	264	**0.27**	**< 0.001**
	1833	4	147	510	**0.29**	**< 0.001**
	1838	2	86	184	0.47	0.417
	1847	4	153	223	**0.69**	**< 0.001**
	1851	1	106	218	0.49	0.735
	1857	2	186	355	0.52	0.396

∗ Chapter III ∗

Do song dialects influence social learning in the zebra finch (*Taeniopygia guttata*)?



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Do song dialects influence social learning in the zebra finch (*Taeniopygia guttata*)?

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ABSTRACT

Several songbird species exhibit geographical variation of song or dialects, and it has been suggested that dialects might facilitate group cohesion. Although song dialects have not been observed in wild populations of zebra finches (*Taeniopygia guttata*), we succeeded to create artificial song dialects under laboratory conditions. Here, we tested the hypothesis that song dialects constitute a group signature that can influence social learning in this species. We exposed male and female observers to two demonstrators singing two different song dialects: one singing the observer's colony's dialect and the other one singing a different song dialect, and each demonstrator eating only one of two types of dyed seeds, both unknown to the observer. We expected the observer to copy the food choice of the demonstrator singing his/her colony's dialect, regardless of their familiarity. Our results did not confirm this hypothesis. Other factors that could have influenced social learning such as demonstrators' song production or feeding activity did not affect the results. In the light of previously published studies, we discuss our results arguing that a more thorough control of those factors is needed when investigating social learning in this model species.

Keywords: social learning; dialect; vocal signature; zebra finch; food choice copying

CHAPTER III

INTRODUCTION

Social learning is defined as learning that is influenced by observation of, or interaction with another animal (typically a conspecific) (Box, 1984; Galef, 1988; as cited in: Heyes, 1994). This definition can be applied to vocal learning, which refers to the ability to modify the features of vocal signals as a result of experience with the vocalizations of others (Janik & Slater, 2000). Vocal learning is quite rare in the animal kingdom, and besides humans (Bruner, 1981; Hauser et al., 2002), it has only been found in few taxonomic groups of mammals (Cetaceans: Janik, 2014; Bats: Boughman, 1998; Elephants: Stoeger & Manger, 2014; Pinnipeds: Reichmuth & Casey, 2014) and in three groups of birds: hummingbirds, parrots and oscine songbirds, a taxon belonging to the passeriformes which represent almost half of the bird species on earth (Bolhuis et al., 2010). In songbird species, vocal learning in the natal zone can lead to the establishment of geographically delimited song types, also called song dialects that can be maintained over long periods of time (Derryberry, 2011; Garcia et al., 2015; Harbison et al., 1999; Marler & Tamura, 1962; Trainer, 1983). It was proposed that song dialects could be a functionless epiphenomenon of vocal learning, without any behavioural salience (Andrew, 1962; Goodfellow & Slater, 1986). Other authors proposed that dialects act as an assortative mating tool (Tomback & Baker, 1984), leading to local genetic adaptations (Marler & Tamura, 1962, 1964; Nottebohm, 1969, 1972). Dialects could also represent social markers (Feekes 1977; Payne, 1981). This last function has received recent attention and it has been proposed that birdsong dialects could signal group identity (Briefer et al., 2008; Hausberger et al., 2008). Thereby, song dialects could have a major impact on highly social species, as in the case of European starlings (*Sturnus vulgaris*): shared vocalizations could increase group cohesion when searching for a nest site, a shelter or for food (Hausberger et al., 2008).

CHAPTER III

The aim of this study was to test the function of dialects as social markers in another highly social species: the zebra finch (*Taeniopygia guttata*). Among songbirds, the zebra finch has been one of the most extensively studied species. In the zebra finch, both males and females emit calls to regulate social interactions within the group or the pair (D'Amelio et al., 2017; Elie et al., 2010, 2011; Vignal et al., 2004, 2008; Zann, 1996), but only males sing. They learn to sing during a sensitive period of their early life, between 25- and 90-days post-hatch (dph) (Immelmann, 1969), by listening, memorizing and reproducing the song of conspecifics. Past these 90 days, the song is crystallised meaning that very few vocal changes are observed thereafter (Immelmann, 1969). Under natural conditions, the song constitutes an individual signature (Clayton, 1988; Cynx & Nottebohm, 1992), as each male zebra finch sings a unique song. It has been suggested that in wild populations, dispersal to and from colonies prevent the formation of song dialects (Zann, 1993) and that in domesticated populations, a high rate of learning errors may prevent the establishment of colony-specific versions of the song (Lachlan et al., 2016). Nevertheless, we succeeded to create artificial song dialects by selecting male founders of three different colonies that produced a very good imitation of a same song model. In such colonies, male offspring developed songs with a high conformity to the song model, each different song model leading to a different dialect (see chapter I of this thesis).

In zebra finches, song is involved in sexual selection, by influencing female choice and predicting males' attractivity (Campbell & Hauber, 2010; Clayton, 1988, 1990; Holveck & Riebel, 2007; Riebel, 2000; Riebel et al., 2002; but see Wang et al., 2017). In this context, we recently showed that song dialects might influence female preferences in zebra finches, with females preferring their native song dialect over a different one (see chapter II of this thesis). However, it has never been demonstrated whether song dialects may constitute a signature that could impact group cohesion in this species. Here, we investigated this issue by means of a social learning experiment.

Beyond vocal learning, social learning is an important mechanism for individuals to obtain adaptive information about their environment and has been often associated with group-living (Krebs et al., 1972; Mason & Reidinger, 1981; but see Lefebvre et al., 1996). Social learning is widely spread in the animal kingdom (Avital & Jablonka, 2000) and has been extensively studied in the foraging context (Danchin et al., 2004). In a context of social foraging, several techniques can be used to obtain food: use of personal information to search for food (producer tactic) or use of social information to exploit resource discoveries of others (scrounger tactic) (Barnard & Sibly, 1981; Giraldeau & Beauchamp, 1999). Additionally, individuals can use social learning to choose what food to eat from, which is often beneficial to avoid a potentially toxic food and consume only safe food sources. This way, social learning allows animals to avoid a potentially costly learning by trial and error (Galef, 1993, 2003; Galef & Giraldeau, 2001; Nicol, 1995; Visalberghi & Addessi, 2003). Indeed, many species forage in group and can express neophobia when facing a novel food source. Young meerkats (*Suricata suricatta*) for instance, are more likely to incorporate a new food into their diet after interacting with experienced conspecifics (Thornton, 2008). Another advantage to use social learning when foraging in groups is to find food more readily than when relying on other sources of information (Boyd & Richerson, 1988; McQuoid & Galef, 1992). In this context, social learning can be considered as a form of information parasitism (Giraldeau et al., 2002), with asocial learners being information "producers" and social learners being information "scroungers" (Laland, 2004).

However, because not all individuals constitute equally reliable sources, an observer will learn more from specific demonstrators than from others, and all observers will not be selective towards the same demonstrator, a phenomenon called directed social learning (Coussi-Korbel & Fragasy, 1995). Several factors can influence social learning, such as the number of demonstrators that express the same behaviour, with a preference for learning the behaviour of

the majority of demonstrators (conformist bias, Lachlan et al., 1998; Pike & Laland, 2010), an effect of dominance (Nicol & Pope, 1994, 1999), familiarity (Benskin et al., 2002; Swaney et al., 2001) or the sex of the demonstrator (Benskin et al., 2002; Katz & Lachlan, 2003). Additionally, in humans as well as in animals, the perception of group belonging can affect social learning (Buttelmann et al., 2013; Esseily et al., 2016; van de Waal et al., 2013). A study carried out by van de Waal et al. (2013) on wild vervet monkeys (*Chlorocebus aethiops*) showed that individuals abandon personal foraging preferences and conform to the group norm when choosing what food to eat from. Additionally, monkeys which migrated to another group that ate an alternative food compared to the group of origin, switched their preference to conform to the new local norm, which underlined the influence of social learning in food choice (van de Waal et al., 2013). In another study on three different species of wild tits (*Cyanistes caeruleus*, *Parus major* and *Poecile palustris*), it has been demonstrated that the social network structure of the population will influence social learning, with individuals having numerous social connexions being more likely to learn about a new foraging source than individuals being less socially connected (Aplin et al., 2012).

Zebra finches are granivorous and forage in flocks to find food resources that are patchily located in time and space (Zann, 1996), which makes social learning an adaptive strategy. Many studies focused on social learning using observer-demonstrator paradigms in this species (Benskin et al., 2002; Guillette & Healy, 2014; Katz & Lachlan, 2003; Riebel et al., 2012; Rosa et al., 2012). In our study, we hypothesized that song dialects could constitute a group signature. If so, in a social learning experiment, adult observers of both sexes should preferentially learn from a male singing their colony's dialect than a male singing a different dialect. To test this, we used zebra finches from three different colonies: two colonies singing the song dialect A (colony A1 and A2), and one colony (colony B) singing a different song dialect, the song dialect B. As only one colony sang the song dialect B, observers from colony

B were necessarily familiar to the demonstrator that sang their colony's dialect. In contrast, in colony A1 and A2, demonstrators producing an imitation of the same model were taken from the other colony as the observer, so that all observers were unfamiliar to both demonstrators. This allowed us to test for an effect of familiarity on social learning. We predicted that in such a social learning task, zebra finches of both sexes would preferentially learn from a demonstrator singing their colony's dialect, regardless of their familiarity to this demonstrator.

MATERIAL AND METHODS

1) Subjects and rearing conditions

All tested birds hatched in the animal facilities of the University Paris Nanterre. They originated from three different colonies, each of them founded by males originally trained to produce the same song model. Details of founders' training and the creation of colonies has been described elsewhere (see chapter I of this thesis). Shortly, several males were exposed to a unique song model during their sensitive phase of song learning, through different training methods. When adult, we calculated the percentage of similarity between their song and the song model they were trained with, using a semi-automated procedure in SAP 2011 (Sound Analysis Pro software; Tchernichovski et al., 2000). We only selected males that produced a close-to-perfect copy of the song model to be founders of the colonies. Colony A1 and A2 were founded by males singing the song model A (Figure 1A). Colony B was founded by males singing a different song model, the song model B (Figure 1A). In a previous experiment, we showed that each song model led to the establishment of a specific dialect in the colonies (see chapter I of this thesis).

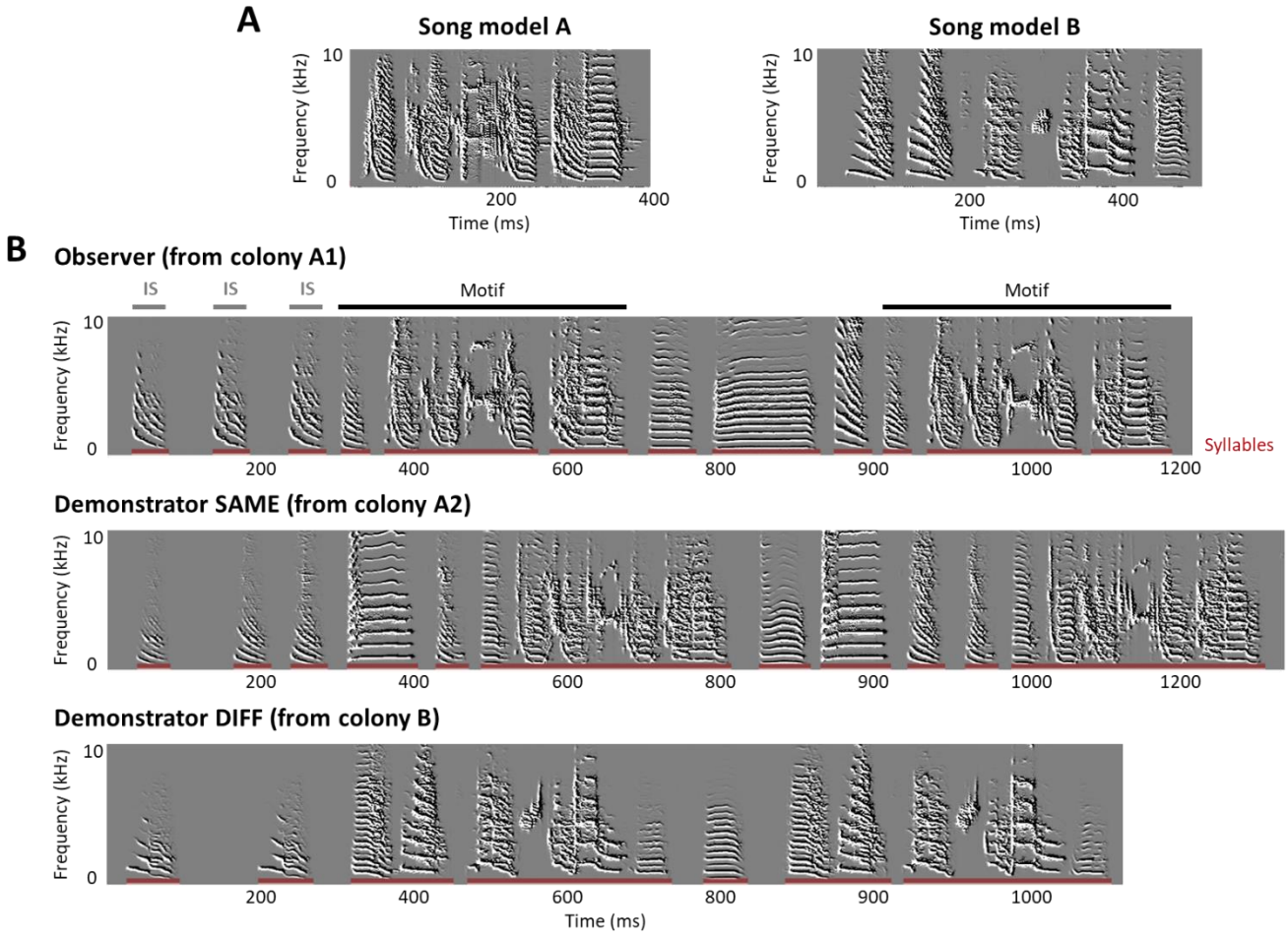

Figure 1. Spectrograms of colonies' song models and of three different males used in the social learning test. (A) Spectrograms of song model A and B that were used to create artificial song dialects. (B) Spectrograms of three male songs: in this example, a male observer from colony A1 was tested with a demonstrator singing the same dialect as his natal colony (demonstrator SAME, from colony A2) and a demonstrator singing a different dialect (demonstrator DIFF, from colony B). In the first spectrogram, different units of a typical zebra finch song are indicated. Syllables are underlined in red, motifs are overlined in black and introductory syllables (IS) in grey.

Colonies were maintained in three distinct aviaries (3.18 x 3.32 x 2.84 m) placed in separated rooms. Colonies were thus visually and acoustically isolated from each other, so that the birds could not hear other songs than the songs produced by the males of their colony. All aviaries were set to a 14:10 light:dark schedule and maintained between 20 and 23°C. Birds had *ad libitum* access to water, a commercial tropical seed mixture hereafter referred to as the "usual

seeds mix" including millet seeds and egg food for exotic finches, as well as sand and cuttlebones. The usual diet was supplemented once a week with vegetables and fruits, and once a month with hard-boiled eggs.

In the social learning experiment, we tested 42 male and 64 female observers: 12 males and 9 females from colony A1, 10 males and 19 females from colony A2 and 20 males and 36 females from colony B (Table 1). In a pilot study, we tested a potential preference for a specific colour of seeds using 12 males from the large pool of birds maintained in our laboratory. colour of seeds using 12 males from the large pool of birds maintained in our laboratory.

2) Experimental set-up

Experiments were conducted in sound-proof chambers (85 x 65 x 60 cm) equipped with fans providing a low airflow in the chamber and lights set on the same photoperiodic schedule as the birds experienced in the aviaries. In each chamber we placed two metal cages (41 x 24 x 34 cm), one in front of the other and separated by 17 cm. Two Logitech C920 webcams were placed in each chamber to monitor the birds' behaviour in each of the two cages. Cameras were connected to ContaCam 4.9.9 software on a DELL Optilex 9020 computer with Windows 7.

One of the two cages is referred to as the "observer" cage and the other as the "demonstrators" cage (Figure 2A). Each cage was arranged in a specific way. The observer cage was equipped with two perches (separated by 8 cm) in the middle part of the cage, that allowed the observer to access two transparent experimental seed dispensers. During certain test phases (see below), the bird could also have access to two standard cage seed cups, containing the usual seeds mix, which were placed in the lower part of the cage. The cage was also equipped with a fountain, providing water *ad libitum*. Birds were familiar to all types of feeders (dispensers and cups). The demonstrators' cage was divided in two equally sized

compartments (20.5 x 24 x 34 cm) by a metal grid, in order to house two different birds. In each part of the cage, two perches separated by 8 cm allowed access to two experimental seed dispensers. During certain test phases, in each part of the cage, one standard cage seed cup was placed in the lower part of the cage. A water fountain was permanently present in each compartment. All cage floors were covered with paper to facilitate regular cleaning that was necessary to ensure that the birds could not feed from seeds scattered on the cage floor.

During the entire experiment, the birds' song activity was continuously recorded using SAP 2011 (Tchernichovski et al., 2000) ran by a DELL Optilex 9020 PC on Windows 7. Each sound-proof chamber was equipped with a Behringer C-2 microphone placed above the cages and connected to a PreSonus AudioBox (24 bit/96K) recording interface.

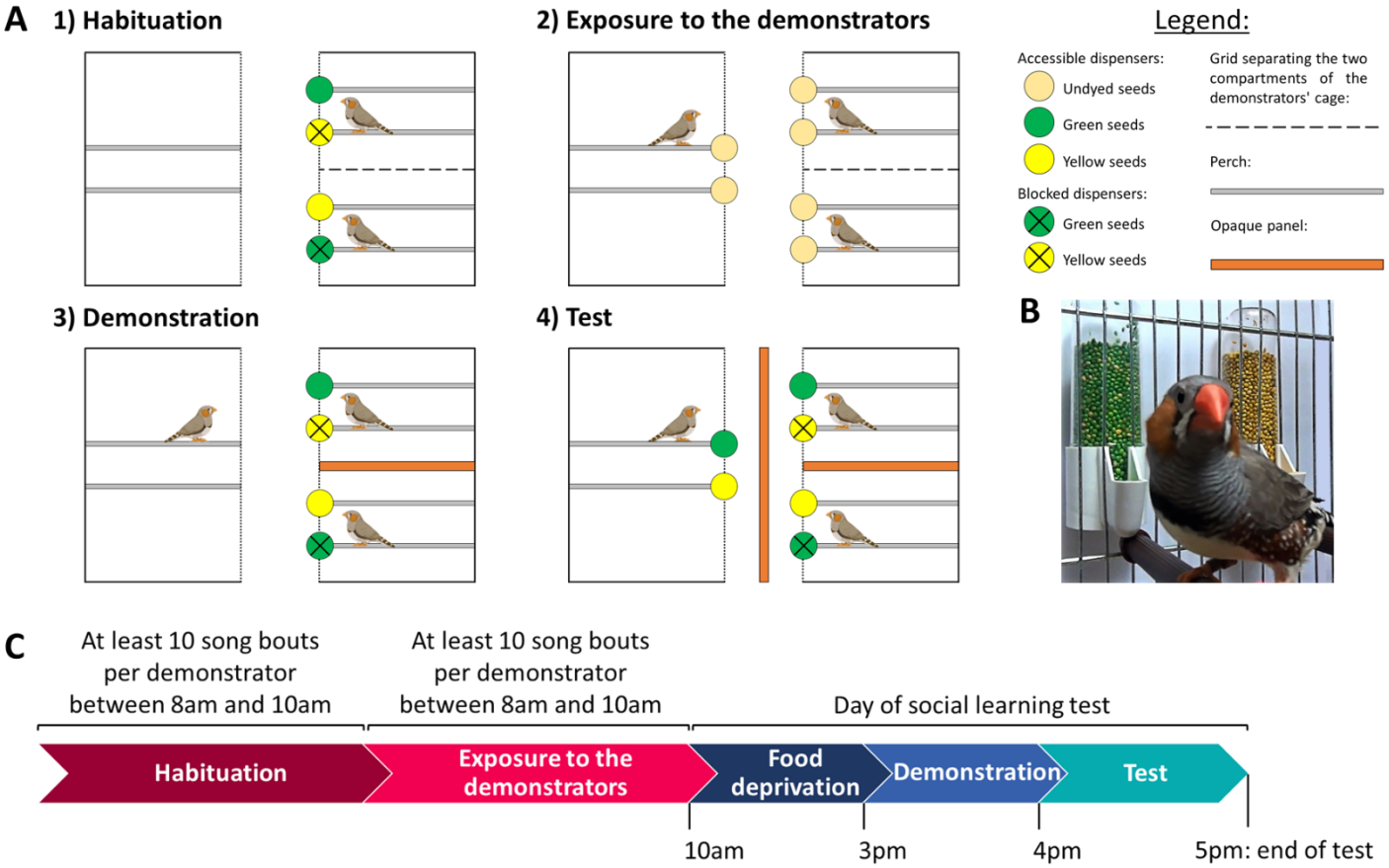

Figure 2. Experimental set-up and timeline. (A) Top view of the experimental set-up for the four different phases of the social learning experiment. The observer's cage is on the left, the demonstrators' cage is on the right. Note the mismatch of perspectives: the top view of cages is combined with lateral views of the birds. (B) Picture of a male observer in front of the two dispensers containing dyed millet seeds. (C) Experimental timeline with the different phases.

3) Seed dyeing

Undyed, natural-coloured millet seeds were dyed using water-soluble food colouring powders with no flavours, of the brand Déco'Relief. The red dye contained azorubine (E122) and indigo carmine (E132). The blue dye contained patent blue V (E131). The green dye contained quinoline yellow (E104) and patent blue V (E131). The yellow dye contained tartrazine (E102). For each colour, 1.2 kg of millet seeds were immerged in 1.5 l of water with

25 g of dye, for 3 hours. Seeds were then drained and spread on a grid covered with absorbent paper, until they were completely dry.

4) Colour preference test

Before starting the social learning test, we checked whether finches would exhibit a preference for a specific colour of seeds, without any social demonstration. Because Muth and collaborators (2013) found no food colour preference between yellow, blue or red seeds, we decided to test birds with two of these three colours. Tested males were food-deprived for six hours and then each male was exposed to two experimental seed dispensers filled with dyed seeds. One dispenser contained 50 g of blue millet seeds, and the other one, 50 g of red millet seeds. The bird's behaviour was recorded for an hour. We analysed the data the same way as described in the section "behaviour of the observer" (see below). We found that males ate significantly more red seeds than blue seeds (Wilcoxon, $Z = -2.84$, $p < 0.01$). So, we repeated the same test with yellow versus green seeds, and we found no significant preference for one of this two colours (Wilcoxon, $Z = -0.08$, $p = 0.97$). Therefore, we kept green and yellow millet seeds for the social learning test.

5) Social learning test

Table 1 summarises the three possible triads of birds within an experimental set-up. We define a "triad" as the three birds that were put together in the same sound-proof chamber: a triad was composed of one observer (male or female) and two male demonstrators.

Table 1. Three possible bird triads within a sound-proof chamber and sample sizes. SAME: demonstrator with the same song dialect as the observer; DIFF: demonstrator with a song dialect that was different from that of the observer.

Observer's colony	n	Observer's familiarity to the demonstrators	SAME demonstrator's colony	DIFF demonstrator's colony
A1	12 males 9 females	Unfamiliar	A2	B
A2	10 males 19 females	Unfamiliar	A1	B
B	20 males 36 females	Familiar with SAME demonstrator	B	A1 or A2

a) Test of male observers

i. <u>Phase 1: habituation</u>

Two male demonstrators were placed in the demonstrators' cage (one in each compartment) on day 1 of the experiment: one male from colony A1 or A2, and one male from colony B. Therefore, each tested bird (hereafter called "the observer") was exposed to a demonstrator singing the same song dialect as his own (hereafter called "SAME" demonstrator) and a demonstrator singing a different song dialect (hereafter called "DIFF" demonstrator). Each demonstrator could access three feeders: two experimental seed dispensers filled with undyed millet seeds, and one standard cage cup containing the usual seeds mix. From day 2 of the experiment, the cup was removed from each compartment between 10 am and 5 pm so that the demonstrator got used to feed from the experimental seed dispensers containing now dyed millet seeds. For each demonstrator, the seed flow of one of the two dispensers containing dyed

seeds was blocked using plastic wrap. Therefore, even if the dyed seeds were visible, no seed could be eaten from the blocked dispenser. This way, each demonstrator could only eat seeds of one specific colour: green or yellow (Figure 2A). The position of the accessible dispenser, either on the right or on the left perch, and the colour of seeds that each demonstrator was able to eat were determined by randomly choosing amongst all the possible combinations (see below in section "choice of demonstrators' and dispensers' placement in the apparatus"). During the habituation phase, the dispensers' positions were swapped every day to avoid a side bias and make sure that the demonstrators learned that they could only feed from one of the two dispensers containing dyed seeds.

Each day, the song activity of both demonstrators was assessed by counting the number of songs, with a visual inspection of spectrograms using the Sound Explorer 2011 software. A typical zebra finch song is produced in bouts: each song bout usually starts by introductory syllables, followed by one or several renditions of the motif (Figure 1B). The motif is defined as a short and stereotyped sequence of syllables, syllables being sounds that are separated from each other by silent gaps (Hyland Bruno & Tchernichovski, 2017; Williams, 1990; Williams & Staples, 1992; Zann, 1996) (Figure 1B). When both males sang a minimum of ten song bouts between 8 am (when the lights switched on) and 10 am, we considered that song activity was sufficient, and the observer was introduced in the sound-proof chamber (Figure 2C). If song activity was not sufficient, both male demonstrators were left in the apparatus for another day until at least ten song bouts were produced by each of them between 8 am and 10 am.

ii. Phase 2: observer's exposure to the demonstrators

Before putting the future observer in the sound-proof chamber with the two demonstrators, the demonstrators' experimental seed dispensers containing dyed seeds were replaced with dispensers containing undyed ones, so that the observer would not be visually

exposed to the dyed seeds prior to the test (Figure 2A). The observer was placed in the observer cage, facing the demonstrators' cage (Figure 2A). At this point, the observer could access the experimental seed dispensers containing undyed millet seeds and the standard cage cups containing the usual seeds mix. At 2 pm, we visually isolated the observer from the demonstrators with an opaque panel. Observer and demonstrators could now only interact vocally. Like the day before, the demonstrators' undyed seeds were replaced by dyed seeds, so that they continued to feed only from one specific dispenser. The standard seed cups of the observer were removed so he could get used to feed from the experimental seed dispensers. At 5 pm, the dyed seed dispensers of the demonstrators were replaced by undyed seed dispensers, the standard seed cups were put back for both the demonstrators and the observer, and the opaque panel was removed.

The social learning test required that the observer had been sufficiently exposed to the song of both demonstrators. Therefore, the day following the introduction of the observer, the songs that were recorded in the morning (between 8 am and 10 am) were assessed. If both demonstrators sang a minimum of ten song bouts while in presence of the observer, the social learning test started (Figure 2C; see section below). If not, all three birds were left in the same conditions, and the same procedure as described before was repeated until there was a sufficient song activity in both demonstrators. The three birds were left together for a maximum of 3 days before the observer was tested.

iii. Phase 3 & 4 - Social learning preference test: demonstration and test

The three birds were food-deprived at 10 am (Figure 2C). We ensured that all tested birds were food deprived the same amount of time so that their motivation to feed was equal, since previous work demonstrated that this could affect the tendency to learn socially (Dorrance & Zentall, 2001). At 3 pm, the social demonstration phase of the test began and lasted for an

hour (Figure 2C). For the demonstration, the two demonstrators were visually isolated from each other by an opaque panel (Figure 2A). Thus, during the demonstration phase, the observer could see the two demonstrators, but each demonstrator could only see the observer. In each demonstrator's compartment, we placed the two experimental seed dispensers containing dyed seeds, with only one of the two dispensers being accessible (as in the habituation phase) (Figure 2A). Using video monitoring, we checked that the demonstrators fed from the dyed seeds in presence of the observer. At the end of the demonstration (4 pm), the observer was visually isolated from the demonstrators by an opaque panel and the test phase began (Figure 2A).

Two accessible dispensers were placed in the observer's cage: one containing yellow seeds and one containing green seeds (Figure 2A & 2B). The position of the yellow and green dispensers (on the right or left perch) was determined by randomly choosing amongst all the possible combinations (see below in section "choice of demonstrators' and dispensers' placement in the apparatus"). The test phase lasted for one hour (Figure 2C). At the end of the test phase, dispensers with dyed seeds were replaced by dispensers filled with undyed seeds and the standard cage seed cups were reintroduced.

After the test phase, the male observer became a demonstrator for another observer. This way, we formed new pairs of demonstrators, who started a new phase of habituation in another sound-proof chamber. Each male was used as a demonstrator twice at most, before being reintroduced in his colony. To start this experiment, we used six demonstrators (three A2 males and three B males) who therefore could never be tested as observers.

iv. Choice of demonstrators' and dispensers' placement in the apparatus

In the apparatus, we could select: 1) the position of the SAME/DIFF demonstrator in the cage; 2) the colour of seeds that were accessible to the SAME/DIFF demonstrator; 3) the

position of the yellow/green dispenser for each demonstrator (SAME and DIFF) and for the observer. A set of 32 possible combinations of these options was established (Table S1). For each observer, one combination among the 32 was selected randomly. A previously selected combination could not be re-used before all of 32 combinations were picked once.

b) Test of female observers

Female observers were tested following the same procedure as the male observers. As females could not become demonstrators, when the test was finished, the female observer was transferred in her colony's aviary and another female was introduced in the apparatus. So, the only difference with the protocol used for male observers concerned the use of the demonstrators: the same dyad of demonstrators with the same placement combination could be used for a maximum of four different female observers. Once the demonstrator dyad had been used for four females, males were transferred in their respective colonies. In total, 22 different demonstrator dyads were used to test the female observers.

6) Data analysis

On the 42 tested males, six had to be excluded from the analysis: two for logistical reasons and four that ate less than ten seeds during the testing phase. Over the 64 tested females, eight had to be excluded: three for logistical reasons and five that ate less than ten seeds during the testing phase. The final sample is therefore composed of 36 males and 56 females.

a) Behaviour of the observer

All video recordings were analysed using BORIS v.5.1.0. We measured the latency to ingest the first seed and the number of ingested seeds for 15 min after the first ingested seed, and for the total duration of 1h of test. During the coding, we differentiated whether the observer was ingesting a seed from the dispenser containing the same seed colour that was accessible to

the SAME demonstrator: “SAME seed”; or was ingesting a seed from the dispenser containing the same seed colour that was accessible to the DIFF demonstrator: “DIFF seed”.

b) Behaviour of the demonstrators

i. Feeding activity

We coded the demonstrators’ feeding activity in the same way as for the observers. For the following analysis, we considered the number of seeds ingested by the demonstrators during the entire hour of demonstration. The analyses related to the demonstrators' feeding activity were conducted on a subset of 35 male observers and 26 female observers.

ii. Song activity

Using the Sound Explorer software, we counted the number of produced motifs by each demonstrator. This was done visually for the entire time the observer was exposed to the demonstrator. In this study we also analysed a smaller part of this song activity dataset and looked at the song activity of demonstrators only on the day of test. For both tests on males and females, we found a significant positive correlation between the number of motifs produced by a demonstrator during the day of test and the whole period of exposition to the observer (experiment with male observers: $r_s = 0.56$, $p < 0.001$; experiment with female observers: $r_s = 0.83$, $p < 0.001$). We therefore considered only the song data on the entire period of exposition for the following analyses. The analyses related to the demonstrators’ song activity were conducted on a subset of 32 male observers, and on 56 female observers (all tested females).

7) Statistical analysis

The number of seeds eaten by the birds might reflect more how hungry they were, than their actual preference strength. Therefore, for each observer, we measured his or her preference

ratio for the colour of seeds that was eaten by a specific demonstrator and ran the statistical tests on those ratios. At the population level, we tested whether there was a significant preference to learn from a specific demonstrator in both experiments (on male and on female observers). To this end, we checked whether the median preference ratio of the observers for the colour of seeds eaten by a given demonstrator was greater than by chance, that is, we compared it to 0.5 using single sample Wilcoxon signed rank tests.

To test our main hypothesis concerning the effect of song dialect on social learning, we calculated the preference ratio of each observer for the SAME demonstrator: number of SAME seeds eaten/total number of seeds eaten. To test the effect of familiarity to the SAME demonstrator, we ran a generalized linear model (GLM) for the male experiment and a generalized mixed model (GLMM) for the female experiment. In each of these two models, we tested whether the preference ratio of observers for the colour of seeds eaten by their SAME demonstrator differed according to their familiarity with this SAME demonstrator (familiar or unfamiliar). For each observer, the response variable was weighted by the total number of eaten seeds (using the *weights* parameter). Because several females were exposed to the identical SAME demonstrator, for the GLMM on females, we included the number (ID) of the SAME demonstrator the female was tested with, as a random effect. We checked for overdispersion and because we detected overdispersion in both models, we used error distributions from the quasi family: quasibinomial distribution and a logit link function. The GLM on male observers was performed using the *glm* function from the *stats* package in R and the GLMM on female observers using the *glmmPQL* function from the *MASS* package.

We hypothesized that beside the song dialect of both demonstrators, their respective behaviour such as their song activity and feeding activity could have influenced the propensity of the observer to copy their food choice. To check for an effect of the song activity or feeding

activity of the demonstrator on the observer's social learning, we created categories within each demonstrators' dyad, regardless of whether the demonstrator was a SAME or a DIFF demonstrator. For the song activity, we distinguished the demonstrator which produced more motifs within the dyad (SONG+), from the demonstrator that produced fewer motifs (SONG-). For the feeding activity, we also distinguished the demonstrator which ate more seeds (SEED+) from the demonstrator which ate fewer seeds (SEED-). For each observer, we calculated: 1) the preference ratio for the demonstrator that sang more (SONG+): number of seeds eaten of the same colour as the one eaten by the demonstrator SONG+/total number of seeds eaten, and 2) the preference ratio for the demonstrator that ate more (SEED+): number of seeds eaten of the same colour as the one eaten by the demonstrator SEED+/total number of seeds eaten. When assigning demonstrators to these categories we neglected the magnitude of differences in singing or feeding activity. Because the size of this difference could also have had an impact on the observers' choice of demonstrator to learn from, we calculated: 1) the proportion of motifs produced by the demonstrator that sang more within the demonstrators' dyad (number of motifs produced by the demonstrator SONG+/total number of motifs heard by the observer), and 2) the proportion of seeds eaten by the demonstrator that ate more within the demonstrators' dyad: number of seeds eaten by the demonstrator SEED+/total number of seeds eaten by the two demonstrators. We controlled whether these proportions were correlated with the preference ratio of the observer using Spearman's correlations.

RESULTS

Concerning the food choice of the observers, we found the same results for the two different observation periods (15 min from the first ingested seed or one hour of test). Thus, as in Katz & Lachlan (2003), we focused our analysis on a relatively short period following the social demonstration: here, we present the results obtained from the first 15 min after the

observer ingested the first seed. On average, male observers ate 77 ± 44 seeds and female observers ate 72 ± 48 seeds in 15 min. On average, male observers took less than two minutes (mean ± SD: 1 min 30 s ± 3 min 28 s) to ingest their first seed. For 20 out of 36 male observers, the first ingested seed was of the same colour as the one eaten by the SAME demonstrator. This first choice did not significantly differ from a random distribution (binomial test: $p = 0.62$). We found similar results for the females: female observers ate their first seed after 3 min 12 s ± 4 min 28 s, and 24 out of 56 females ingested a first seed from the same colour as the one eaten by their SAME demonstrator, which was not significantly different from chance level at the population level (binomial test: $p = 0.35$). Additionally, we noticed that a few birds were highly selective in their food choice: 7 out of 36 males consumed exclusively seeds from the same colour as eaten by the SAME demonstrator and 2 exclusively from the same colour as eaten by the DIFF demonstrator. In total, 20 males ate more SAME seeds than DIFF seeds, 15 males ate more DIFF than SAME seeds and one male ate the same amount of SAME and DIFF seeds. We found the same pattern in females: 9 out of 56 females exclusively ingested SAME seeds and 8 exclusively DIFF seeds. In total, 27 females consumed more SAME than DIFF seeds, 28 females consumed more DIFF than SAME seeds and one consumed the same amount of SAME and DIFF seeds. We also tested whether the median preference ratio of observers for the SAME seeds was significantly different from 0.5. This was not the case neither for male nor for female observers (males: $V = 373$, $p = 0.34$; females: $V = 796$, $p = 0.83$), indicating that observers did not preferentially learn from the SAME demonstrator rather than the DIFF demonstrator (Figure 3). All together, these results show that there is no preference to ingest seeds of the same colour as the one eaten by the SAME demonstrator.

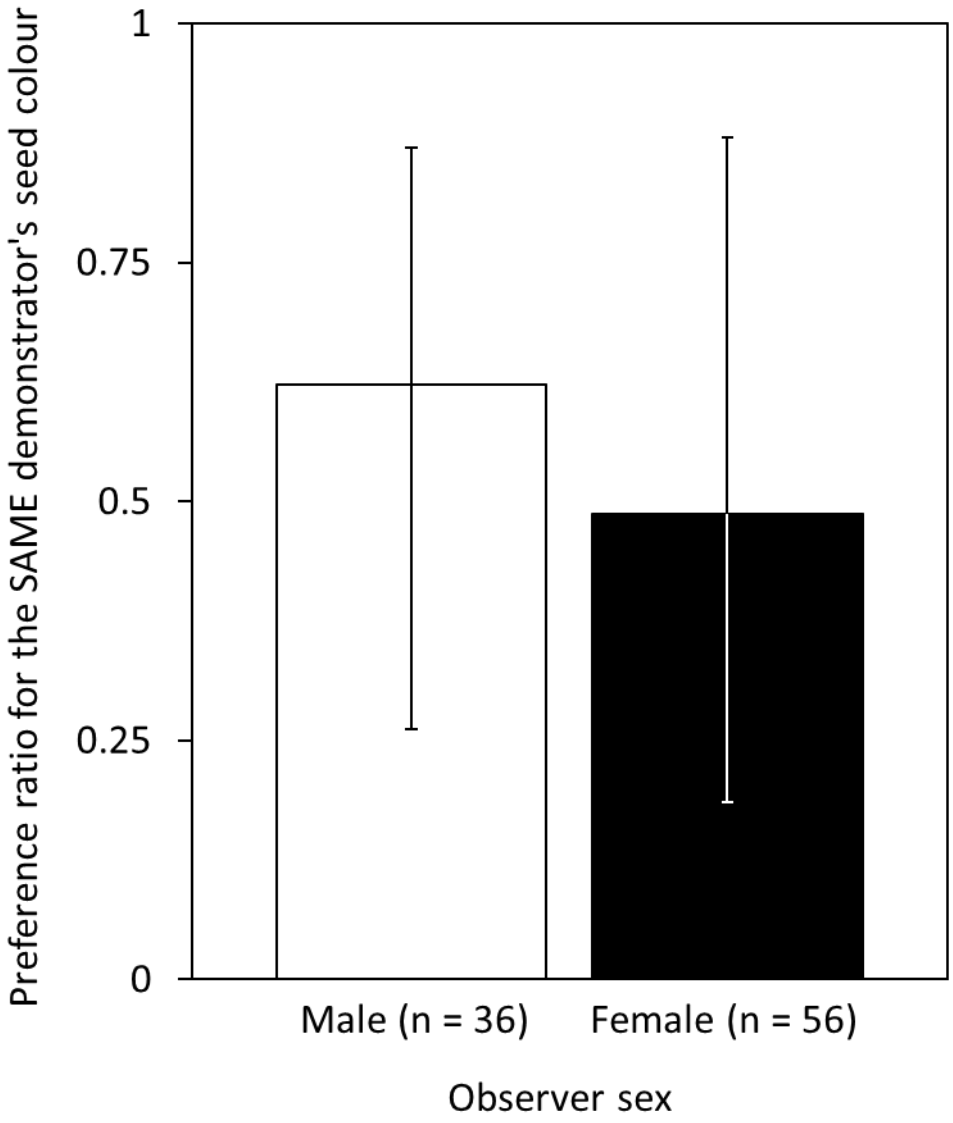

Figure 3. Effect of song dialect on social learning in the food preference test. At random, observers would be expected to feed equally from the two different seed colours (0.5 preference ratio). The histograms show the median preference ratio for the seed colour that was eaten by the SAME demonstrator singing a song corresponding to their colony's dialect. Error bars represent interquartile ranges. Male and female observers did not significantly eat more seeds from the colour that was eaten by their SAME demonstrator than expected by chance.

Because observers from colony B were familiar to their SAME demonstrator whereas observers from colony A1 and A2 were not, we then investigated whether the familiarity to the SAME demonstrator could have an effect on the propensity of the observer to learn from this demonstrator. We did not find any significant effect of the familiarity to the SAME

demonstrator on the preference ratio for this demonstrator, neither for males nor for female observers (males: estimate ± SE = -0.60 ± 0.49, $p = 0.23$; females: estimate ± SE = -0.07 ± 0.52, df = 32, $p = 0.89$). This suggests that the proportion of SAME seeds the observer ingested do not differ according to whether the SAME demonstrator was familiar or unfamiliar to the observer.

Because the type of song (corresponding to the colony's dialect or different from the colony's dialect) sung by the demonstrators and the familiarity to the SAME demonstrator did not seem to influence the food choice of observers, we then tested for potential effects of the demonstrators' behaviour on the observer's response: the effect of song activity and feeding activity. Neither in male nor in female observers did we find a significant difference from the 0.5 level in the median preference ratio for the demonstrator SONG+ (males: V = 179, $p = 0.18$; females: V = 607, $p = 0.17$; Table 2). This suggests that observers did not prefer to eat seeds of the same colour as the demonstrator which sang more, compared to the one which sang less (SONG-). We then verified whether the proportion of song heard from the demonstrator which sang more, relative to the total amount of song heard during the exposition to both demonstrators could influence the food choice of the observer. We found no significant correlation between the proportion of song sung by the demonstrator that sang more (SONG+) and the proportion of seeds eaten by the observer of the same colour as the one eaten by the demonstrator SONG+, neither in male observers ($r_s = 0.08$, $p = 0.66$), nor in females ($r_s = -0.14$, $p = 0.3$).

Concerning the effect of the demonstrators' feeding activity, we did not find any significant difference from 0.5 in the median preference ratio for the demonstrator that ate more seeds (SEED+), in any of the two experiments (males: V = 277, $p = 0.73$; females: V = 195, $p = 0.62$; Table 2). This indicated that the observers did not eat more seeds of the same colour as

the demonstrator SEED+, compared to the demonstrator that ate less (SEED-). Additionally, we checked whether the proportion of seeds eaten by the demonstrator SEED+ over the total number of seeds eaten by both demonstrators influenced the observer's food choice. We found no significant correlation between the proportion of seeds eaten by the demonstrator SEED+ and the preference ratio of the observer for seeds of the same colour as the ones eaten by the demonstrator SEED+ (males: r_s = -0.05, p = 0.75; females: r_s = -0.05, p = 0.78). All together, these results suggest that differences in song activity or feeding activity between the two demonstrators were unlikely to affect the degree to which observers copied their food choice.

Table 2. Effects of the demonstrators' song activity and feeding activity on the observer's preference ratio. For the song activity, the median represents the preference ratio for the seed colour that was eaten by the demonstrator which sang more (SONG+). For the feeding activity, the median represents the preference ratio for the seed colour that was eaten by the demonstrator which ate more (SEED+). Each median was compared to a random level of 0.5 using single sample Wilcoxon tests. IQR account for interquartile ranges.

						Single sample Wilcoxon test	
Demonstrators' behaviour	Observer's sex	n	Median	Lower IQR	Upper IQR	V	*p*-value
Song activity	Male	32	0.29	0.05	0.72	179	0.18
	Female	56	0.38	0.10	0.70	607	0.17
Feeding activity	Male	35	0.50	0.10	0.77	277	0.73
	Female	26	0.44	0.23	0.95	195	0.62

DISCUSSION

In the wild, there is no report that zebra finches exhibit geographical variation of song or dialects. In the laboratory, we succeeded to create artificial song dialects (see chapter I of

this thesis). Our main hypothesis in the current study that zebra finches would preferentially learn from an individual singing their colony's dialect was not validated by our results. Thus, we cannot conclude on whether song could act as an affiliative signal in a social learning task of foraging. Additionally, we did not find that the familiarity to the demonstrator influenced the propensity of the observer to learn from him. This result contrasts with those of another study showing that male zebra finches preferred the food hopper from which their familiar demonstrator had fed (Benskin et al., 2002).

In our study, neither the type of song nor the familiarity affected the observers' response. Therefore, we also controlled for potential effects of the demonstrators' behaviour on the degree to which observers copied their food choices. We first controlled for an effect of song activity, as it has been done by Benskin and collaborators (2002). Similarly to what they found, our observers did not significantly learn more from the demonstrator which sang more or the one which sang less, showing that song activity did not affect the food choice of the observer. We then controlled for an effect of feeding activity of both demonstrators. Indeed, it has been found that the relative feeding activity of a demonstrator could affect social learning in zebra finches, with females learning more from a female demonstrator rather than a male, but only if the female demonstrator ate less than its male counterpart (Katz & Lachlan, 2003). However, our results did not show a significant effect of the demonstrators' feeding activity: observers of both sexes did not learn preferentially from the demonstrator which ate more than the other, or the one which ate less. In addition, the observer’s food choice was not influenced by the perceived relative difference in the song rate or feeding rate of the two demonstrators.

Previous studies emphasised the importance of the observer's sex in social learning about food choice, with females usually being more sensitive to social learning than males (Benskin et al., 2002; Guillette & Healy, 2014; Katz & Lachlan, 2003). Methods applied in the

current study were comparable to those previous ones. However, we did not find an effect of sex, as results concerning male and female observers were comparable.

Even though our results provide more evidence for the random pattern of behavioural transmission (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985), there is substantial evidence that social learning experiments with a food choice paradigm are an effective way of assessing food choice copying in the zebra finch, and that the transmission of food choice is non-random but rather biased by social preferences and relationships (Benskin et al., 2002; Guillette & Healy, 2014; Katz & Lachlan, 2003; Riebel et al., 2012). In our study, the vast majority of tested birds ate during the test and some of them were even selective to one colour of seeds. However, it is possible that because observers were food deprived for a slightly longer period of time compared to other studies (usually between 1 and 4 hours: cf. Benskin et al., 2002; Boogert et al., 2008, 2011; Guillette & Healy, 2014; Riebel et al., 2012; but see Katz & Lachlan, 2003: overnight (17h30)), their feeding behaviour was driven more by their hunger rather than a social choice. This could have resulted in a lower selectivity towards food, which could explain why a lot of birds ate both type of seeds. In zebra finches, it also has been shown that the reliance on social information when searching for food varies greatly between individuals and is not entirely flexible (Rosa et al., 2012). Indeed, it appears that individuals that were less active when sampling their environment consistently relied more on social information than more active birds (Rosa et al., 2012). In our laboratory, birds spend their lives in aviaries with all the other birds of their colony and we do not have any information on individual behaviours related to feeding. It is possible that some individuals were used to rely more on personal information to feed and thus did not rely on the social information that could be provided by the demonstrators. Such behaviour could have hidden social preferences of other individuals at the population level. Furthermore, the design of our experiment allowed both demonstrators to feed from a palatable food source, no matter the colour of this food. Thus, the

behaviour of demonstrators did not change after ingesting the millet seeds, contrary to what we could expect after an ingestion of a toxic or distasteful food. Because observers witnessed the feeding behaviour of demonstrators for one hour, we can suspect that even if an observer successfully discriminated between the two song dialects, he/she did not use this information to guide his/her food choice, because both food sources seemed trustworthy. Finally, the absence of preferential social learning from the bird singing the colony's dialect in both female and male observers could be explained by the fact that in the three colonies, despite an overall conformity to the colony's song type, some males produced songs that deviated from it (Derégnaucourt et al., 2014; see chapter I of this thesis). Consequently, some tested females could have been paired to males producing a poor version of the colony's dialect. Mated female zebra finches express a preference for their mate's song; a finding that has been interpreted as indicative of the role of song for pair bond maintenance (Miller, 1979). Therefore, next to strengthening pair bonds, such a preference might also have an impact on food choice copying and might have influenced the female's social learning in this study. Furthermore, some females of colony B might have been tested with their own mate as the SAME demonstrator. Additionally, for male as well as for female observers, a poor imitation of the colony's song dialect by the SAME demonstrator could have mislead the observer and resulted in not identifying the song of this specific demonstrator as the colony's song dialect.

In the current study, familiarity did not affect the social learning of tested zebra finches. However, beyond familiarity, it has been demonstrated that the strength of social relationships between individuals from the same group vary and can impact the diffusion of information within the group (Croft et al., 2008). Aplin et al. (2012) also suggested that an information on a new food patch would be preferentially transmitted between more socially connected individuals. In a similar way, in our study, the decision of an observer on whether to choose the

same food as his familiar demonstrator could have been influenced by the quality of their relationships in the colony, a parameter that we did not assess.

In few studies, the song and feeding activity of demonstrators were controlled (Benskin et al., 2002; Katz & Lachlan, 2003). No effect of song frequency was found (Benskin et al., 2002). However, Katz & Lachlan (2003) found an impact of feeding activity for female zebra finches and discussed this finding in a context of food competition. In several studies, it has been shown that dominance affected social learning in birds: in hens, individuals learn more effectively if exposed to a dominant rather than a subordinate hen (Nicol & Pope, 1994, 1999). Conversely, Katz & Lachlan (2003) suggested that observers might perceive more competition from the individual eating more (dominant individual) and thus learn preferentially from the individual eating less (subordinate individual). Alternatively, the dominant demonstrator spending more time eating, it might leave to the subordinate demonstrator the possibility to interact more with the observer and consequently attract more attention. In the current study, a similar pattern with song activity could have been found, with demonstrators singing more being perceived as dominant individuals. However, since we found no effect of the feeding or song activity on the observers' response, here, we cannot assess a potential effect of dominance.

Other factors that we did not control could have impacted the social learning of zebra finches, either by influencing the perceived dominance within the bird triad or simply by drawing more attention to one demonstrator than to the other. First, in some male triads, we observed song overlapping involving some male observers and the demonstrators (Lucille Le Maguer & Alice Araguas, personal observation). Song overlapping has been suggested to function as a threatening signal in other species (Naguib & Mennill, 2010). Thus, besides an effect of dominance between the two demonstrators that could have influenced the observer’s behaviour as already observed in canaries (Amy & Leboucher, 2009), another relation of

dominance could have been established between one or both demonstrators and the observer. Secondly, female observers emitted calls that could have been directed preferentially to one demonstrator or the other and thus elicited more interactions with one particular demonstrator. Alternatively, females could have called to both demonstrator but one of them engaged more readily in interaction with her. In both cases, such interactions might then have been decisive for social learning. Lastly, during the observer's exposure to demonstrators, the three birds could interact visually as well as vocally. During this time, other behaviours such as threats or movements around the cage (Benskin et al., 2002) could have impacted the food choice of the observer. A more detailed analysis of the triads' behaviour would provide us with clues as to the establishment of dominance relationships between these individuals who could not physically interact. Such an analysis could also inform us about an eventual enhancement of attention by a specific demonstrator.

Finally, some females might have had individual preferences for a male that was not necessarily the one singing the song of her colony, which could have affected their choice of male from whom to copy. Indeed, in the zebra finch as in many species of oscine songbirds, mate choice can be related to a combination of song, morphological signals and courtship displays (Morris, 1954; Williams, 2001) or can be based on characteristic independent of song. Therefore, in our study, females' preference could have been related to different behavioural traits such as levels of aggressiveness (Forstmeier & Birkhead, 2004) and/or personality traits (Schuett et al., 2011), as well as morphological traits (Bennett et al., 1996; Burley & Coopersmith, 1987; Swaddle & Cuthill, 1994).

Using live demonstrators in a social learning experiment did not allow us to disentangle the effect of the colony's dialect from the other characteristics of demonstrators, and this made it difficult to control for all factors that could have potentially affected the observer's response.

In this context, the recent use of video stimuli and robots in this field of research is very appealing. For example, Guillette and Healy (2017) found that a silent video had the same effect on the observers' behaviour as a live demonstration. This provided a scientific validation for the use of a new methodology when testing for social information transfer in a foraging context in the zebra finch (Guillette & Healy, 2017). Similarly to a video stimulus, using a robot demonstrator (Webb, 2008) would allow us to standardize the demonstration phase and present the exact same stimulus to all tested birds (D'Eath, 1998; Oliveira et al., 2000). However, these techniques require the social isolation of the observer, thereby inducing a rise of plasma corticosterone that could modify its behaviour, as suggested by Perez and collaborators (2012). It could be more profitable to test social learning in more natural conditions, i.e. by studying the social transmission of a foraging information within groups (c.f. Aplin et al. 2012; van de Waal et al., 2013).

Because the use of social information depends on the context under which animals copy others (Laland, 2004), we could consider testing the link between social learning and song dialects in another context than the foraging context. For example, researchers found that young male zebra finches that had never constructed a nest, preferred to use the nesting material of the same colour as the one used by the familiar male demonstrator, even if this choice did not provide any particular advantage for the final structure of the nest (Guillette et al., 2016). Interestingly, this study revealed a social preference for a feature which conferred no specific advantage to the social learner, a phenomenon also found in other studies (Aplin et al., 2015; van de Waal et al., 2013).

In humans, language has been described as an important signal of group-membership that drives behavioural imitation (Buttleman et al., 2013), toy choice (Kinzler et al., 2007) or food choice (Shutts et al., 2009). Because in human and non-human animals, culture is

considered as all group-typical behavioural patterns shared by members of communities and that are to some degree reliant on socially-learned and transmitted information (Laland & Janik, 2006), social preferences for arbitrary features in animals might be analogous to human trends and fashion that lead to the establishment of cultures. In our case, if zebra finches would be found to express copying of arbitrary features in relation to their colony's dialect, this would indicate that song dialects indeed constitute a groups signature that could lead to the establishment of cultures.

To conclude, our study is the first to investigate the role of song dialects as a group signature on social learning in zebra finches. Our results raise some main concerns as how to assess such social preferences when multiple factors can influence the observer's response. To clearly identify reliable sources of information that could influence social learning in this model species, further studies should take extra care in controlling for potential confounding factors.

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REFERENCES

Amy, M., & Leboucher, G. (2009). Effects of Eavesdropping on Subsequent Signalling Behaviours in Male Canaries. *Ethology*, *115*(3), 239–246. https://doi.org/10.1111/j.1439-0310.2008.01579.x

Andrew, R. J. (1962). Evolution of Intelligence and Vocal Mimicking. *Science*, *137*(3530), 585–589.

Retrieved from JSTOR.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1745), 4199–4205. https://doi.org/10.1098/rspb.2012.1591

Aplin, Lucy M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*(7540), 538–541.

Avital, E., & Jablonka, E. (2000). *Animal Traditions: Behavioural Inheritance in Evolution*. https://doi.org/10.1017/CBO9780511542251

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, *29*(2), 543–550. https://doi.org/10.1016/S0003-3472(81)80117-0

Bennett, A. T. D., Cuthill, I. C., Partridge, J. C., & Maier, E. J. (1996). Ultraviolet vision and mate choice in zebra finches. *Nature*, *380*(6573), 433–435. https://doi.org/10.1038/380433a0

Benskin, C. M. H., Mann, N. I., Lachlan, R. F., & Slater, P. J. B. (2002). Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, *64*(5), 823–828. https://doi.org/10.1006/anbe.2002.2005

Bolhuis, J. J., Okanoya, K., & Scharff, C. (2010). Twitter evolution: Converging mechanisms in birdsong and human speech. *Nature Reviews Neuroscience*, *11*(11), 747–759. https://doi.org/10.1038/nrn2931

Boogert, N. J., Anderson, R. C., Peters, S., Searcy, W. A., & Nowicki, S. (2011). Song repertoire size in male song sparrows correlates with detour reaching, but not with other cognitive measures. *Animal Behaviour*, *81*(6), 1209–1216.

Boogert, N. J., Giraldeau, L. A., & Lefebvre, L. (2008). Song complexity correlates with learning ability in zebra finch males. *Animal Behaviour*, *76*(5), 1735–1741.

Boughman, J. W. (1998). Vocal learning by greater spear–nosed bats. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1392), 227–233. https://doi.org/10.1098/rspb.1998.0286

Box, H. O. (1984). *Primate Behaviour and Social Ecology*. Springer Science & Business Media.

Boyd, R., & Richerson, P. J. (1985). *Culture and the Evolutionary Process*. University of Chicago Press.

Briefer, E., Aubin, T., Lehongre, K., & Rybak, F. (2008). How to identify dear enemies: The group signature in the complex song of the skylark *Alauda arvensis*. *Journal of Experimental Biology*, *211*(3), 317–326. https://doi.org/10.1242/jeb.013359

Bruner, J. S. (1981). The social context of language acquisition. *Language & Communication*, *1*(2–3), 155–178. https://doi.org/10.1016/0271-5309(81)90010-0

Burley, N., & Coopersmith, C. B. (1987). Bill Color Preferences of Zebra Finches. *Ethology*, *76*(2), 133–151. https://doi.org/10.1111/j.1439-0310.1987.tb00679.x

Buttelmann, D., Zmyj, N., Daum, M., & Carpenter, M. (2013). Selective Imitation of In-Group Over Out-Group Members in 14-Month-Old Infants. *Child Development*, *84*(2), 422–428. https://doi.org/10.1111/j.1467-8624.2012.01860.x

Campbell, D. L. M., & Hauber, M. E. (2010). Behavioural correlates of female zebra finch (*Taeniopygia guttata*) responses to multimodal species recognition cues. *Ethology Ecology & Evolution*, *22*(2), 167–181. https://doi.org/10.1080/03949371003707885

Cavalli-Sforza, L. L., & Feldman, M. W. (1981). *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton University Press.

Clayton, N. S. (1988). Song discrimination learning in zebra finches. *Animal Behaviour*, *36*(4), 1016–1024. https://doi.org/10.1016/S0003-3472(88)80061-7

Clayton, N. S. (1990). Subspecies recognition and song learning in zebra finches. *Animal Behaviour*, *40*(6), 1009–1017. https://doi.org/10.1016/S0003-3472(05)80169-1

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*(6), 1441–1453. https://doi.org/10.1016/0003-3472(95)80001-8

Croft, D. P., James, R., & Krause, J. (2008). *Exploring Animal Social Networks*. Princeton University Press.

Cynx, J., & Nottebohm, F. (1992). Role of gender, season, and familiarity in discrimination of conspecific song by zebra finches (*Taeniopygia guttata*). *Proceedings of the National Academy of Sciences*, *89*(4), 1368–1371.

D'Amelio, P. B., Klumb, M., Adreani, M. N., Gahr, M. L., & ter Maat, A. (2017). Individual recognition of opposite sex vocalizations in the zebra finch. *Scientific Reports*, *7*. Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5514125/

Danchin, É., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public Information: From Nosy Neighbors to Cultural Evolution. *Science*, *305*(5683), 487–491. https://doi.org/10.1126/science.1098254

D'eath, R. B. (1998). Can video images imitate real stimuli in animal behaviour experiments? *Biological Reviews*, *73*(3), 267–292. https://doi.org/10.1017/S0006323198005179

Derégnaucourt, S., Nagle, L., Gahr, M., Aubin, T., & Geberzahn, N. (2014). Cultural Evolution of Birdsong in the Laboratory. *Neuroscience Annual Meeting 2014*.

Derryberry, E. P. (2011). Male response to historical and geographical variation in bird song. *Biology Letters*, *7*(1), 57–59.

Dorrance, B. R., & Zentall, T. R. (2001). Imitative learning in Japanese quail (*Coturnix japonica*) depends on the motivational state of the observer quail at the time of observation. *Journal of Comparative Psychology*, *115*(1), 62–67. https://doi.org/10.1037/0735-7036.115.1.62

Elie, J. E., Mariette, M. M., Soula, H. A., Griffith, S. C., Mathevon, N., & Vignal, C. (2010). Vocal communication at the nest between mates in wild zebra finches: A private vocal duet? *Animal Behaviour*, *80*(4), 597–605. https://doi.org/10.1016/j.anbehav.2010.06.003

Elie, J. E., Soula, H. A., Mathevon, N., & Vignal, C. (2011). Dynamics of communal vocalizations in a social songbird, the zebra finch (*Taeniopygia guttata*). *The Journal of the Acoustical Society of America*, *129*(6), 4037–4046. https://doi.org/10.1121/1.3570959

Esseily, R., Somogyi, E., & Guellai, B. (2016). The Relative Importance of Language in Guiding Social Preferences Through Development. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.01645

Feekes, F. (1977). Colony-specific song in Cacicus cela (*Icteridae, Aves*): The password hypothesis. *Ardea*, *65*(3–4), 197–202.

Forstmeier, W., & Birkhead, T. R. (2004). Repeatability of mate choice in the zebra finch: Consistency within and between females. *Animal Behaviour*, *68*(5), 1017–1028.

Galef, B. G. (2003). "Traditional" foraging behaviors of brown and black rats (*Rattus norvegicus and Rattus rattus). The Biology of Traditions: Models and Evidence*, 159–186.

Galef, B. G. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In *Social learning: Psychological and biological perspectives* (pp. 3–28). Hillsdale, NJ, US: Lawrence Erlbaum Associates, Inc.

Galef, B. G. (1993). Functions of social learning about food: A causal analysis of effects of diet novelty on preference transmission. *Animal Behaviour*, *46*(2), 257–265. https://doi.org/10.1006/anbe.1993.1187

Galef, B. G., & Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour*, *61*(1), 3–15. https://doi.org/10.1006/anbe.2000.1557

García, N. C., Arrieta, R. S., Kopuchian, C., & Tubaro, P. L. (2015). Stability and change through time in the dialects of a Neotropical songbird, the Rufous-collared Sparrow. *Emu*, *115*(4), 309–316.

Giraldeau, L., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*. Retrieved from https://royalsocietypublishing.org/doi/abs/10.1098/rstb.2002.1065

Giraldeau, L. A., & Beauchamp, G. (1999). Food exploitation: Searching for the optimal joining policy. *Trends in Ecology & Evolution*, *14*(3), 102–106. https://doi.org/10.1016/S0169-5347(98)01542-0

Goodfellow, D. J., & Slater, P. J. (1986). A model of bird song dialects. *Animal Behaviour*, *34*(5), 1579–1580. https://doi.org/10.1016/S0003-3472(86)80233-0

Guillette, L. M., & Healy, S. D. (2014). Mechanisms of copying behaviour in zebra finches. *Behavioural Processes*, *108*, 177–182. https://doi.org/10.1016/j.beproc.2014.10.011

Guillette, L. M., & Healy, S. D. (2017). The roles of vocal and visual interactions in social learning zebra finches: A video playback experiment. *Behavioural Processes*, *139*, 43–49. https://doi.org/10.1016/j.beproc.2016.12.009

Guillette, L. M., Scott, A. C. Y., & Healy, S. D. (2016). Social learning in nest-building birds: A role for familiarity. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827), 20152685. https://doi.org/10.1098/rspb.2015.2685

Harbison, H., Nelson, D. A., & Hahn, T. P. (1999). Long-Term Persistence of Song Dialects in the Mountain White-Crowned Sparrow. *The Condor*, *101*(1), 133–148. https://doi.org/10.2307/1370454

Hausberger, M., Bigot, E., & Clergeau, P. (2008). Dialect use in large assemblies: A study in European starling *Sturnus vulgaris* roosts. *Journal of Avian Biology*, *39*(6), 672–682.

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, *298*(5598), 1569–1579. https://doi.org/10.1126/science.298.5598.1569

Heyes, C. M. (1994). Social Learning in Animals: Categories and Mechanisms. *Biological Reviews*, *69*(2), 207–231. https://doi.org/10.1111/j.1469-185X.1994.tb01506.x

Holveck, M. J., & Riebel, K. (2007). Preferred songs predict preferred males: Consistency and repeatability of zebra finch females across three test contexts. *Animal Behaviour*, *74*(2), 297–309.

Hyland Bruno, J., & Tchernichovski, O. (2017). Regularities in zebra finch song beyond the repeated motif. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2017.11.001

Immelmann, K. (1969). Song development in the zebra finch and other estrildid finches. *Bird Vocalizations*, *61*.

Janik, V. M. (2014). Cetacean vocal learning and communication. *Current Opinion in Neurobiology*, *28*, 60–65. https://doi.org/10.1016/j.conb.2014.06.010

Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, *60*(1), 1–11. https://doi.org/10.1006/anbe.2000.1410

Katz, M., & Lachlan, R. F. (2003). Social learning of food types in zebra finches (*Taenopygia guttata*) is directed by demonstrator sex and feeding activity. *Animal Cognition*, *6*(1), 11–16. https://doi.org/10.1007/s10071-003-0158-y

Kinzler, K. D., Dupoux, E., & Spelke, E. S. (2007). The native language of social cognition. *Proceedings*

of the National Academy of Sciences, *104*(30), 12577–12580. https://doi.org/10.1073/pnas.0705345104

Krebs, J. R., MacRoberts, M. H., & Cullen, J. M. (1972). Flocking and feeding in the great tit *parus major* – an experimental study. *Ibis*, *114*(4), 507–530. https://doi.org/10.1111/j.1474-919X.1972.tb00852.x

Lachlan, R. F., Crooks, L., & Laland, K. N. (1998). Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, *56*(1), 181–190. https://doi.org/10.1006/anbe.1998.0760

Lachlan, R. F., van Heijningen, C. A., ter Haar, S. M., & ten Cate, C. (2016). Zebra Finch Song Phonology and Syntactical Structure across Populations and Continents—A Computational Comparison. *Frontiers in Psychology*, *7*. Retrieved from http://www.ncbi.nlm.nih.gov/pmc/articles/PMC4935685/

Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, *32*(1), 4–14. https://doi.org/10.3758/BF03196002

Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, *21*(10), 542–547.

Lefebvre, L., Palameta, B., & Hatch, K. K. (1996). Is Group-Living Associated With Social Learning? A Comparative Test of a Gregarious and a Territorial Columbid. *Behaviour*, *133*(3–4), 241–261. https://doi.org/10.1163/156853996X00134

Marler, P., & Tamura, M. (1962). Song 'Dialects' in Three Populations of White-Crowned Sparrows. *The Condor*, *64*(5), 368–377. https://doi.org/10.2307/1365545

Marler, P., & Tamura, M. (1964). Culturally transmitted patterns of vocal behavior in sparrows. *Science*, *146*(3650), 1483–1486.

Mason, J. R., & Reidinger, R. F. (1981). Effects of Social Facilitation and Observational Learning on Feeding Behavior of the Red-Winged Blackbird (*Agelaius phoeniceus*). *The Auk*, *98*(4), 778–784. https://doi.org/10.1093/auk/98.4.778

McQuoid, L. M., & Galef, B. G. (1992). Social influences on feeding site selection by Burmese fowl (*Gallus gallus*). *Journal of Comparative Psychology*, *106*(2), 137–141.

https://doi.org/10.1037/0735-7036.106.2.137

Miller, D. B. (1979). The acoustic basis of mate recognition by female zebra finches (*Taeniopygia guttata*). *Animal Behaviour*, *27*, 376–380.

Morris, D. (1954). The Reproductive Behaviour of the Zebra Finch (*Poephila guttata*), with Special Reference to Pseudofemale Behaviour and Displacement Activities. *Behaviour*, *6*(4), 271–322.

Muth, F., Steele, M., & Healy, S. D. (2013). Colour preferences in nest-building zebra finches. *Behavioural Processes*, *99*, 106–111. https://doi.org/10.1016/j.beproc.2013.07.002

Naguib, M., & Mennill, D. J. (2010). The signal value of birdsong: Empirical evidence suggests song overlapping is a signal. *Animal Behaviour*, *80*(3), e11–e15.

Nicol, C. J. (1995). The social transmission of information and behaviour. *Applied Animal Behaviour Science*, *44*(2), 79–98. https://doi.org/10.1016/0168-1591(95)00607-T

Nicol, C. J., & Pope, S. J. (1994). Social learning in small flocks of laying hens. *Animal Behaviour*, *47*(6), 1289–1296. https://doi.org/10.1006/anbe.1994.1177

Nicol, C. J., & Pope, S. J. (1999). The effects of demonstrator social status and prior foraging success on social learning in laying hens. *Animal Behaviour*, *57*(1), 163–171. https://doi.org/10.1006/anbe.1998.0920

Nottebohm, F. (1969). The song of the chingolo, *Zonotrichia capensis*, in Argentina: Description and evaluation of a system of dialects. *The Condor*, *71*(3), 299–315.

Nottebohm, F. (1972). The Origins of Vocal Learning. *The American Naturalist*, *106*(947), 116–140. https://doi.org/10.1086/282756

Oliveira, R. F., Rosenthal, G. G., Schlupp, I., McGregor, P. K., Cuthill, I. C., Endler, J. A., Fleishman, L.J., Zeil, J., Barata, E., Burford, F., Gonçalves, D., Haley, M., Jakobsson, S., Jennions, M.D., Körner, K.E., Lindström, L., Peake, T., Pilastro, A., Pope, D.S., Roberts, S.G.B., Rowe, C., Smith, J., & Waas, J. R. (2000). Considerations on the use of video playbacks as visual stimuli: The Lisbon workshop consensus. *Acta Ethologica*, *3*(1), 61–65. https://doi.org/10.1007/s102110000019

Payne, R. B. (1981). Population structure and social behaviour: Models for testing the ecological

significance of song dialects in birds*: In: Alexander RD & Tinkle DW (eds): Natural selection and social behaviour: Recent Research and New Theory*. Chiron Press. New York: 108.

Perez, E. C., Elie, J. E., Soulage, C. O., Soula, H. A., Mathevon, N., & Vignal, C. (2012). The acoustic expression of stress in a songbird: Does corticosterone drive isolation-induced modifications of zebra finch calls? *Hormones and Behavior*, *61*(4), 573–581. https://doi.org/10.1016/j.yhbeh.2012.02.004

Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, *6*(4), 466–468. https://doi.org/10.1098/rsbl.2009.1014

Reichmuth, C., & Casey, C. (2014). Vocal learning in seals, sea lions, and walruses. *Current Opinion in Neurobiology*, *28*, 66–71. https://doi.org/10.1016/j.conb.2014.06.011

Riebel, K. (2000). Early exposure leads to repeatable preferences for male song in female zebra finches. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1461), 2553–2558.

Riebel, K., Smallegange, I. M., Terpstra, N. J., & Bolhuis, J. J. (2002). Sexual equality in zebra finch song preference: Evidence for a dissociation between song recognition and production learning. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1492), 729–733. https://doi.org/10.1098/rspb.2001.1930

Riebel, K., Spierings, M. J., Holveck, M. J., & Verhulst, S. (2012). Phenotypic plasticity of avian social-learning strategies. *Animal Behaviour*, *84*(6), 1533–1539. https://doi.org/10.1016/j.anbehav.2012.09.029

Rosa, P., Nguyen, V., & Dubois, F. (2012). Individual differences in sampling behaviour predict social information use in zebra finches. *Behavioral Ecology and Sociobiology*, *66*(9), 1259–1265. https://doi.org/10.1007/s00265-012-1379-3

Schuett, W., Godin, J. G. J., & Dall, S. R. X. (2011). Do Female Zebra Finches, *Taeniopygia guttata*, Choose Their Mates Based on Their 'Personality'? *Ethology*, *117*(10), 908–917. https://doi.org/10.1111/j.1439-0310.2011.01945.x

Shutts, K., Kinzler, K. D., McKee, C. B., & Spelke, E. S. (2009). Social Information Guides Infants' Selection of Foods. *Journal of Cognition and Development*, *10*(1–2), 1–17.

https://doi.org/10.1080/15248370902966636

Stoeger, A. S., & Manger, P. (2014). Vocal learning in elephants: Neural bases and adaptive context. *Current Opinion in Neurobiology*, *28*, 101–107. https://doi.org/10.1016/j.conb.2014.07.001

Swaddle, J. P., & Cuthill, I. C. (1994). Female zebra finches prefer males with symmetric chest plumage. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *258*(1353), 267–271. https://doi.org/10.1098/rspb.1994.0172

Swaney, W., Kendal, J., Capon, H., Brown, C., & Laland, K. N. (2001). Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, *62*(3), 591–598. https://doi.org/10.1006/anbe.2001.1788

Tchernichovski, O., Nottebohm, F., Ho, C. E., Pesaran, B., & Mitra, P. P. (2000). A procedure for an automated measurement of song similarity. *Animal Behaviour*, *59*(6), 1167–1176. https://doi.org/10.1006/anbe.1999.1416

Thornton, A. (2008). Social learning about novel foods in young meerkats. *Animal Behaviour*, *76*(4), 1411–1421. https://doi.org/10.1016/j.anbehav.2008.07.007

Tomback, D. F., & Baker, M. C. (1984). Assortative mating by white-crowned sparrows at song dialect boundaries. *Animal Behaviour*, *32*(2), 465–469. https://doi.org/10.1016/S0003-3472(84)80282-1

Trainer, J. M. (1983). Changes in Song Dialect Distributions and Microgeographic Variation in Song of White-Crowned Sparrows (*Zonotrichia leucophrys nuttalli*). *The Auk*, *100*(3), 568–582. https://doi.org/10.1093/auk/100.3.568

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent Social Learning and Conformity Shape a Wild Primate's Foraging Decisions. *Science*, *340*(6131), 483–485. https://doi.org/10.1126/science.1232769

Vignal, C., Mathevon, N., & Mottin, S. (2004). Audience drives male songbird response to partner's voice. *Nature*, *430*(6998), 448–451.

Vignal, C., Mathevon, N., & Mottin, S. (2008). Mate recognition by female zebra finch: Analysis of individuality in male call and first investigations on female decoding process. *Behavioural Processes*, *77*(2), 191–198. https://doi.org/10.1016/j.beproc.2007.09.003

Visalberghi, E., & Addessi, E. (2003). Food for thought: Social learning about food in capuchin monkeys. *The Biology of Traditions: Models and Evidence*, 187–212.

Wang, D., Forstmeier, W., & Kempenaers, B. (2017). No mutual mate choice for quality in zebra finches: Time to question a widely held assumption. *Evolution*, *71*(11), 2661–2676.

Webb, B. (2008). Chapter 1 Using Robots to Understand Animal Behavior. In *Advances in the Study of Behavior*,38, 1–58. https://doi.org/10.1016/S0065-3454(08)00001-6

Williams, H. (1990). Models for song learning in the zebra finch: Fathers or others? *Animal Behaviour*, *39*(4), 745–757. https://doi.org/10.1016/S0003-3472(05)80386-0

Williams, H. (2001). Choreography of song, dance and beak movements in the zebra finch (*Taeniopygia guttata*). *Journal of Experimental Biology*, *204*(20), 3497–3506.

Williams, H., & Staples, K. (1992). Syllable chunking in zebra finch (*Taeniopygia guttata*) song. *Journal of Comparative Psychology*, *106*(3), 278.

Zann, R. A. (1993). Variation in song structure within and among populations of Australian zebra finches. *The Auk*, 716–726.

Zann, R. A. (1996). *The zebra finch: A synthesis of field and laboratory studies* (Vol. 5). Oxford University Press.

SUPPLEMENTARY MATERIAL

Table S1. Table of the 32 possible combinations according to the SAME demonstrator's position, the colour of accessible seeds, and the position of the dyed seeds for both demonstrators and for the observer. Each position is indicated relative to the bird's point of view.

Combination	Position of SAME demonstrator in the cage	Accessible seed colour for		Position yellow feeder for		
		SAME demonstrator	DIFF demonstrator	SAME demonstrator	DIFF demonstrator	Observer
1	Left	Yellow	Green	Left	Left	Left
2	Left	Green	Yellow	Left	Left	Left
3	Right	Yellow	Green	Left	Left	Left
4	Right	Green	Yellow	Left	Left	Left
5	Left	Yellow	Green	Left	Left	Right
6	Left	Green	Yellow	Left	Left	Right
7	Right	Yellow	Green	Left	Left	Right
8	Right	Green	Yellow	Left	Left	Right
9	Left	Yellow	Green	Right	Left	Left
10	Left	Green	Yellow	Right	Left	Left
11	Right	Yellow	Green	Right	Left	Left
12	Right	Green	Yellow	Right	Left	Left
13	Left	Yellow	Green	Right	Left	Right
14	Left	Green	Yellow	Right	Left	Right
15	Right	Yellow	Green	Right	Left	Right
16	Right	Green	Yellow	Right	Left	Right
17	Left	Yellow	Green	Left	Right	Left
18	Left	Green	Yellow	Left	Right	Left
19	Right	Yellow	Green	Left	Right	Left
20	Right	Green	Yellow	Left	Right	Left
21	Left	Yellow	Green	Left	Right	Right
22	Left	Green	Yellow	Left	Right	Right
23	Right	Yellow	Green	Left	Right	Right
24	Right	Green	Yellow	Left	Right	Right
25	Left	Yellow	Green	Right	Right	Left
26	Left	Green	Yellow	Right	Right	Left
27	Right	Yellow	Green	Right	Right	Left
28	Right	Green	Yellow	Right	Right	Left
29	Left	Yellow	Green	Right	Right	Right
30	Left	Green	Yellow	Right	Right	Right
31	Right	Yellow	Green	Right	Right	Right
32	Right	Green	Yellow	Right	Right	Right

General Discussion

I) GENERAL DISCUSSION AND FUTURE DIRECTIONS

The zebra finch is a renowned biological model that has been extensively studied in the laboratory, especially concerning the social and neurobiological basis of vocal learning (Derégnaucourt, 2011; Immelmann, 1962; Zann, 1996). The zebra finch song has also been established as a tractable model to study the evolution of vocal culture (Fehér et al., 2009). If Fehér and collaborators (2009) used males raised in acoustic isolation during the sensitive period for song learning, here we used males that sang an imitation of the same song in three different colonies. The predictions arising from such an artificial design was that the song would not evolve at random but would rather follow specific patterns determined by social forces guiding song learning. In this context, the observed song variations would then have biological significances for the birds in several aspects of their social lives, such as female preferences and social learning. The aim of this thesis was to provide new insights to better understand the dynamics of cultural evolution in general and cultural evolution of communication signals in particular.

1) Summary of the main findings, interpretations and limits

a) Cultural evolution of birdsong in the laboratory

The first chapter of this thesis concerned the evolution of song within three colonies of zebra finches founded by males originally trained to produce an imitation of the same song model. In two of the three colonies, the founder males learned the same song model (song model A) and in the third colony, founder males were trained to produce a different song model (the song model B). By conducting acoustic analysis of the song of each male offspring that hatched within the three colonies, we tracked the evolution of song through time. Additionally, we compared the three colonies between them but also with a so-called wild-type group in which

males were raised with several potential tutors singing different song types. Finally, to check whether the fidelity with which pupils imitated the song model could be linked to early social interactions (Carouso-Peck & Goldstein, 2019; Clayton, 1987; Derégnaucourt & Gahr, 2013; Jones & Slater, 1996; Tchernichovski & Nottebohm, 1998; Williams, 1990), we conducted observations of social behaviours in the aviaries during the sensitive phase of song learning.

The first and main result of this study is that in such extreme conditions, song dialects can emerge in the zebra finch, in contrast to what has been suggested by Lachlan and collaborators (2016). Indeed, each song model led to different acoustic specificities. Because birds of the three colonies came from the same genetic background and were raised in the same environmental conditions, we conclude that those group dialects constituted distinct vocal cultures. Of course, this experiment was not designed to be generalised to wild zebra finches because birds could not migrate from one colony to another. Thus, we cannot verify or dismiss the proposition made by Zann (1993) that wild zebra finches are unable to create or maintain song dialects because of the extensive dispersal between groups.

The second major finding of this study is that not all song units evolved in the same way. In this study we analysed the zebra finch song at different time scales and found that the constitutive unit – the song motif – remained pretty similar to the song motif of the original song model, with a tendency to simplify over time, showing an important conformity between birds. Such a simplification of the transmitted information over time has already been described in cultural evolution of artificial language in humans (Kirby et al., 2008). On the other hand, we discovered that birds introduced some variability at the macroscopic level of the song structure – i.e. the song bout – by producing varying numbers and types of connector syllables. Song in the zebra finch carries an individual signature (Clayton, 1988; Cynx & Nottebohm, 1992; Williams, 1990). Thus, we suspected that such interindividual variability in the song bout

would help the birds to reinforce their individual signature, which could facilitate vocal recognition and coordination between individuals during vocal interactions. However, using operant conditioning, it was recently found that individual vocal recognition in zebra finches relies more on song syllable structure than on song syllable order (Geberzahn & Derégnaucourt, in preparation), therefore challenging the previous interpretation.

Birdsong learning is under the control of a genetic program that interacts with social factors and experience in shaping birdsong learning (Mets & Brainard, 2018). For example, regarding birdsong learning in zebra finches, different individuals can use various strategies to reach the same outcome, i.e. to imitate the same song (Liu et al., 2004). Song imitation can also be inhibited by social factors, such as the number of male siblings: in zebra finches, the greater the number of male siblings, the lesser the father's song imitation is accurate (Tchernichovski & Nottebohm, 1998). More recently, studies focusing on neuronal coding of species song identity (Araki et al., 2016) and errors in singing performance (Gadagkar et al., 2016) suggest the existence of a balance between innate and acquired aspects of song (Tchernichovski & Lipkind, 2016). Such balance would enable cultural transmission of song, together with the retention of a species-specific signature over generations (Tchernichovski & Lipkind, 2016). Indeed, even though birds are genetically predisposed to produce species-specific features of song, it has been shown that the innate template of song learning could be influence by experience: zebra finches fostered by Bengalese finch parents (*Lonchura striata domestica*) learned Bengalese finch's song syllable morphology, but adjusted durations of inter-syllabic gaps toward the temporality of a classical zebra finch song (that they never heard) (Araki et al., 2016). Finally, a study of Mets & Brainard (2018) showed that despite a major heritable genetic contribution to the variations in song tempo between different Bengalese finch individuals, the importance of heritability depended on social factors, i.e. the quality of song training – either through computer tutoring or live social tutoring –. Therefore, because experience and genetics

act together in shaping birdsong learning and determining interindividual differences in learned song (Mets & Brainard, 2018), such balanced forces could have influenced the song evolution within our colonies such as the interindividual variability at the bout level as well as the quality of imitation of the song model. Indeed, even though our birds came from the same genetic background, some genetic constraints could have determined song learning accuracy, such as genetic mutations affecting their ability to reproduce the song model or to innovate, and genetic factors interacting with social factors to create interindividual variability in the song bout. Additionally, there might be some genetic predispositions to become a "good learner". To sum up, different aspects of song learning could be influenced by the interaction of genetics and social experience during the sensitive period.

Our results also suggest that conformity and variability could be expressed at different levels of the song structure and that they are complementary rather than mutually exclusive in shaping the song of zebra finches. In this context, we consider that our results follow the balancing mechanism proposed by Tchernichovski and colleagues (2017) for polymorphic cultures (Figure 2), with imitation and innovation/copy errors shaping the evolution of birdsong at the same time. Results presented in this thesis provide the first demonstration that different units of the song structure can be shaped differentially by cultural evolution. They provide important new insights for the field of song studies in general and zebra finch song studies in particular. Indeed, they underline the importance of investigating the different units of song structure in order to really be able to capture all changes that could reflect important cultural aspects of vocal learning.

Our results underline the importance of assessing the song bout structure when focusing on song learning and the evolution of song in the zebra finch, but still little is known about the actual value and significance of this song unit for young birds learning to sing. We assessed

song bout structure through the number of connector types produced by pupils as well as through the linearity, consistency and stereotypy scores representing how the song bout structure was organised and reflecting its stereotypy (Scharff & Nottebohm, 1991; Iyengar & Bottjer, 2002; Kao & Brainard, 2006; Zevin et al., 2004). In future studies, additional methods could be used to analyse the song bout structure, providing new insights on how the song learning took place in the artificial colonies and how the song evolved from founder males to late-hatched pupils. The first method that could be helpful is the raster plot analysis, a technique that has been widely used in the study of birds' vocalisations (Derégnaucourt et al., 2009; Lipkind & Tchernichovski, 2011; Hyland Bruno & Tchernichovski, 2017). It consists in representing the envelope of the acoustic signal, extracted from the sound amplitude and in aligning numerous song bouts on the same syllable to visualise each male's "song bout profile" (Figure 6).

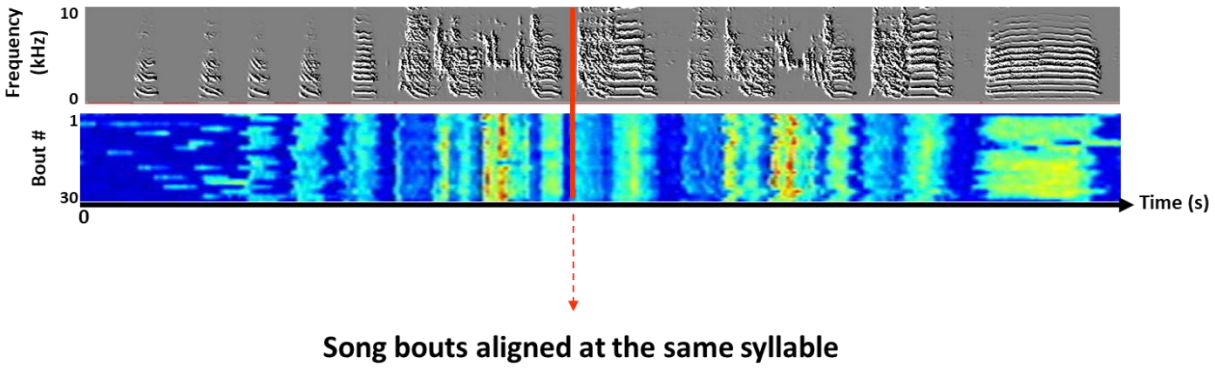

Figure 6. Illustration of a raster plot of a zebra finch song. The upper panel represents a spectrogram of a zebra finch song bout and the lower panel represents the raster plot obtained from several song bouts produced by this bird. The envelope of the acoustic signal is extracted from the sound amplitude and 30 song bouts are aligned at the same syllable and placed one under the other to reveal the males' "song bout profile".

The second method that could be useful focuses on the combinatorial structure of the song bout and consists in transition matrices of motif-connection types (number of connectors between motifs) (Hyland Bruno & Tchernichovski, 2017). Finally, a third method that could be

applied to the study of song bout structure is syntax analysis, namely the analysis of the order of song syllables within the song bout, assessed through transition diagrams (Menyhart et al., 2015; Okanoya, 2004). As a recent study showed that zebra finches tend to prioritize an effective learning of syllable vocabulary rather than an efficient syntax learning (Lipkind et al., 2017), such analysis could better inform us on how cultural evolution shape the different levels of the zebra finch song.

We only focused our acoustic analyses on the song, but it is known that distance calls are also learned by male zebra finches (Zann, 1990). Distance calls are usually produced by pair members when visually isolated (Zann, 1996). They have several functions such as kin (Zann, 1990) and mate (Vignal et al., 2004, 2008) recognition, as well as a function to regulate social interactions within groups (Elie et al., 2011). Therefore, it would be interesting to conduct analyses on male calls to track the potential evolution of call specificities over time in the three colonies, as we did for the song.

Finally, we did not identify any clear relation between social interactions and song learning in the colonies. This finding is not in line with studies showing that the juveniles' choice of tutor can be influenced by their social interactions with potential tutors (Clayton, 1987; Jones & Slater, 1996; Williams, 1990). Our findings rather suggest that in zebra finches, social interactions with adult males but also with peers (Derégnaucourt & Gahr, 2013; Tchernichovski & Nottebohm, 1998), and females (Carouso-Peck & Goldstein, 2019) could shape song learning. However, there are limits to these results, concerning the timing and duration of the observations. For instance, we could not track all social interactions of male pupils that occurred during their entire sensitive phase of song learning. It has been demonstrated that the quantity and quality of social relationships as well as the social structure of a population can be captured by social network analysis (Boogert et al., 2014). Such analysis

is facilitated by the rapid emergence of technologies to track individual behaviours in social environments (Dell et al., 2014; cited in: Ljubicic et al., 2016). Individual tracking in free-flying rooms has already been used in zebra finches, with passive integrated transponder (PIT) tags detected by radio-frequency identification (RFID) (e.g. Boogert et al., 2014; Boucaud et al., 2016; Mariette & Griffith, 2012). However, this technique does not allow researchers to track "moment-to-moment" social interactions of birds within the network as detection by RFID is confined to defined localisations such as feeders. Studying vocal learning with a similar approach would require continuous recordings of vocalisations (potentially with individual wireless microphones; Gill et al., 2015), tracking 3D location and heading (direction), as well as detecting non-vocal gestures (Ljubicic et al., 2016), with techniques that have already been used in several species and some in songbirds (for a review, see Ljubicic et al., 2016).

b) Birdsong dialects and female preferences

The emergence of zebra finch song dialects in controlled laboratory conditions opens new ways to look at the functions of vocal culture and its evolution. In the context of intersexual selection, we focused on the influence of song dialects on female zebra finches' preferences. All tested females hatched in the three previously created colonies and only heard one song type during their early life: the song dialect of their native colony. Using an operant test device, females could either trigger the playback of a song stimulus corresponding to their own colony song type, or a zebra finch song different from their colony song type, both songs being sung by unfamiliar males. The results showed that within each colony, most females had a preference for their colony song type over the song type that differed from their natal dialect. However, at the group level, the preference for the local song dialect was reflected only in one colony. Those results confirm what has been found in several studies, namely that female zebra finches express a preference for the songs heard early in life (Clayton, 1988; Miller, 1979a; Riebel, 2000; Riebel

et al., 2002) and that they are capable of generalising their learned preference to an unfamiliar male's song (Clayton, 1990; Riebel, 2009). However, the current study is the first to propose that song dialects could matter for female zebra finches even if only weak song variations have been described in wild populations of zebra finches (Zann, 1993). We propose that such a preference could play a role in the emergence and stability of song dialects, as it has been suggested in other species exhibiting vocal cultures (Baker & Cunningham, 1985; O'Loghlen & Rothstein, 1995, 2003; Payne et al, 1981; Rothstein & Fleischer, 1987), with females being able to guide the pupils' song learning (Carouso-Peck & Goldstein, 2019) towards the colony song type.

One limit of this study lays in the fact that females' preference for the colony song type was not reflected at the population level. As discussed in chapter II, this could be explained by some specific sound characteristics of certain non-colony song type stimuli that might have been preferred by females. Furthermore, we found differences in the preference ratio and motivation to peck between the colonies, with females of the first colony (A1) exhibiting a higher preference ratio for the colony song type and a higher number of pecks than females of the third colony (B). As discussed in chapter II, these results could also be due to differences in females' adult experience with song (Béguin et al., 1998; Clayton, 1988; Miller, 1979b; Nagle & Kreutzer, 1997; Riebel, 2009), i.e. differences in the amount of time that females spent in contact with males during their lives. This points to the importance of keeping the amount of time spent with males constant between different groups.

Despite such limits, our results are similar to studies in other species showing that females prefer their natal song dialect over a foreign one (brown-headed cowbirds: King et al., 1980; O'Loghlen & Rothstein, 1995; Nuttal's white-crowned sparrows: Baker, 1983; Baker et al., 1981: mountain white-crowned sparrows: MacDougall-Shackleton et al., 2001). Therefore,

they could have broader repercussions in the field of song dialect studies, However, such results are usually discussed in the context of sexual selection (Marler & Tamura, 1962, 1964; Nottebohm, 1969, 1972), implying that the female chooses her sexual partner in relation to its song. But in this thesis, we could not verify that the song preference expressed by female zebra finches was really a sexual preference. Indeed, in opposition to photosensitive species in which it is easy to control the breeding period by modifying light duration in the laboratory and in which the females' sexual receptivity can be easily assessed before the test (e.g. in the canary using Copulation Solicitation Displays, nest-building behaviour or egg-laying; Leboucher et al., 2012; Amy et al., 2008), zebra finches lack seasonality in breeding and are considered as opportunistic breeders (Immelmann, 1962; Zann, 1996). Therefore, it is difficult to assess zebra finch females' sexual receptivity behaviourally before testing, making it impossible to disentangle the effects of sexual preference versus social preference. Here, we could not conclude on the nature of the observed female preferences. This constitute one limit of our work. Indeed, the colony song type could be interpreted by females as an affiliative signal rather than a sexual signal raising new questions about the potential role of zebra finches' song dialects in social behaviours such as social learning.

c) Song dialects and social learning

In the last part of this thesis, we wondered whether song dialects could influence social learning in this highly social species. To investigate this issue, we used an observer-demonstrator paradigm that has proven efficient in a context of food choice in this species (Benskin et al., 2002; Guillette & Healy, 2014; Katz & Lachlan, 2003; Riebel et al., 2012). Given that song dialects can signal group identity (Briefer et al., 2008; Hausberger et al., 2008) and possibly influence group cohesion (Hausberger et al., 2008), we expected that a male or a female zebra finch facing novel types of food that come in two unfamiliar colours would be

more likely to copy the food choice of a demonstrator singing the native dialect of their colony rather than a demonstrator singing a foreign dialect. However, this was not validated by our results: even if most observers ate more seeds of one colour compared to the other, neither female nor male observers seemed to have copied the food choice according to the song dialect of the demonstrator. The observers did not predominantly copy the food choice of the demonstrator singing the colony's dialect, but they did not copy the choice of the demonstrator singing the foreign dialect either. Additionally, we examined whether other factors influenced the birds' social learning such as 1) familiarity to the demonstrator singing the colony dialect, 2) the singing activity of both demonstrators and 3) their feeding activity during the demonstration. None of these factors had an impact of the observers' food choice. This study is the first to assess the role of song dialects as a group signature on social learning in zebra finches, but our results could not validate the hypothesis that song dialects could constitute such a group signature and influence social learning. Our findings raise concerns about the difficulty to evaluate social learning when multiple parameters such as dominance between the birds, sexual preference in females, or overall social relationships could influence the observers' behaviour at the same time. In this context, the use of new technologies such as videos (Guillette & Healy, 2017) or animal robots (Webb, 2008) appear as the adequate approach to control for factors acting on social learning in this species.

The observer-demonstrator paradigm seemed to have worked in assessing social learning of food choice in the zebra finch in previous studies. However, one limit of this set-up is that the testing conditions do not correspond to natural conditions in which the copying of food choice usually appears. In our study, all birds were food-deprived, and observers were exposed to two demonstrators feeding at the same time without any change in their respective behaviour, providing no indications that one of the novel food types was inedible. These two components could have influenced the birds' behaviour and would have prevented us to

faithfully measure social learning. To overcome such obstacles, one good alternative would be to conduct social learning experiments in more "natural" conditions. For example, a possibility would be to use a similar procedure as the one described in van de Waal et al. (2013) for wild vervet monkeys (*Chlorocebus pygerythrus*). In their study, authors investigated whether individuals that migrated from a group originally trained to prefer one food colour, to another group where the alternative colour was favoured would switch their previously learned preference (van de Waal et al., 2013). In zebra finches, this could be adapted with groups being the different colonies: it would be possible to train birds to feed exclusively from one colour of seeds and then reintroducing them, either in an aviary in which birds sing the same song type as their native colony, or in an aviary in which birds sing a different song dialect. In both cases, aviaries' birds would only feed from seeds of another colour. This way, we could examine whether a bird reintroduced in a colony singing the native dialect would be more likely to switch his previously learned preference and conform to the local norm than a bird introduced in a colony singing a different song dialect. In this case, this would indicate the existence of social learning related to group signature.

To sum up, the findings that song dialects could emerge in the zebra finch, the related females' preferences and their potential implications on social learning provide an important contribution to the understanding of birdsong cultural evolution. However, they also raised new questions and revealed some new prospects about studying the cultural evolution of birdsong in the laboratory in general and especially in the zebra finch. Future research directions will be outlined below.

2) Direction for future studies

a) Cultural evolution of birdsong in the laboratory

Few studies focus on the potential emergence of vocal culture in the zebra finch even though this species is widely studied in neuroethology and behavioural ecology. This thesis work constitutes one step in understanding the cultural evolution of the zebra finch song in the laboratory. To pursue the investigation of this topic, it would be interesting to repeat the experiment and manipulate different factors that could impact song learning and thus the emergence of song dialects and their evolution through time. For example, we could modify the proportion of founders singing the same song model by having a minority of founders singing a specific song model and a majority singing a different one. We could also use song models that highly differ in their structure and acoustics of the song syllables. With these artificial conditions, it would then be possible to evaluate 1) the potential emergence of song dialects, 2) the speed of song evolution and 3) the implications of experimental variables on different time scales of the song.

Our study is also a strong invitation to repeat our experiment with other close-ended learner species that do not necessarily exhibit a song dialect, in order to provide a broader comprehension of the mechanisms of vocal learning and birdsong evolution.

b) Testing in more natural conditions

The zebra finch is a highly social species. And it has been demonstrated that social isolation often induces behavioural inhibition in social species (Krause & Ruxton, 2002; Martins et al., 2007; Mainwaring et al., 2011; Perez et al., 2012). This could have major implications for example when testing for vocal production, female preference, cognitive abilities or personality traits. Therefore, zebra finch research would benefit from techniques

allowing to test birds in more natural conditions. As mentioned before, the pit tag technology appears as a good method to test birds in semi-natural aviaries, for instance for female preferences. Indeed, in the wild and in the laboratory, this technology has been successfully used to track both male and female zebra finches' nest visits (Boucaud et al., 2016; Mariette & Griffith, 2012). In laboratory conditions, this technique could be used by creating a set up in which aviaries would contain different nest boxes from which different song playbacks could be broadcasted. In this situation, females would be equipped with pit tags, allowing the tracking of nest visits by females, which could reflect their preference for specific songs.

Studying vocal communication of small songbirds in semi-natural aviaries rather than in sound-proof chambers is now also feasible with lightweight wireless microphones (Anisimov et al., 2014; Ter Maat et al., 2014). It has already been used to track call interactions and call dynamics during pair-bond formation in zebra finch groups (Gill et al., 2015), and could potentially be used to study juvenile song development (Ljubicic et al., 2016). Indeed, equipping young zebra finches with microphones during their sensitive phase of song learning would help us understand the dynamics of song learning in communal aviaries. In our case it would have helped us understand the developmental origins of vocal innovations and/or copy errors which could have impacted the song evolution in the colonies. With no doubt, the rapid growth of technologies will make it easier to study various behavioural aspects of laboratory birds in more natural conditions.

c) Social learning and song learning from videos and robots

Video playbacks have already been used successfully in the study of visual communication as well as species and individual recognition in birds (for a review, see Ljubicic et al., 2016). Additionally, video playbacks can induce male directed song (Ikebuchi & Okanoya, 1999) and female courtship behaviour (Swaddle et al., 2006) in zebra finches.

However, only few studies used video playbacks in a learning context (song learning context: Deshpande et al., 2014; social learning of food choice context: Guillette & Healy, 2017) and the results were not entirely conclusive. Ljubicic and collaborators (2016) suggest that the use of video could be used to create virtual social environments, destined to provide a deeper understanding of the song learning mechanisms. For example, they propose that when a young bird sings, the system will detect the pitch of his song and trigger a video playback accordingly: either a video of a female-biased group of birds for a high pitch song or a video of a group with an equal sex ratio for a lower pitch song. This kind of set up would allow to test whether the bird would adjust his song to attract more females (Ljubicic et al., 2016). The authors argue that designing virtual social environments using videos would allow to test social influences on vocal learning and "provide an inroad into the ecological complexity of vocal development without sacrificing experimental control" (Ljubicic et al., 2016).

Even though presented video techniques are very promising, they are not yet fully developed and extensively used. To this date the exposition to video playbacks (either passive or interactive) does not seem to induce an effective learning in the tested birds. This suggests that physical and vocal interactions are needed in a learning situation, at least in zebra finches. This hypothesis could be tested using a bird robot, since it has been suggested that animal robots can be used to understand animal behaviour (Webb, 2008). Non interactive robots have already been used in two bird species to induce courtship behaviour (Patricelli & Krakauer, 2010; Patricelli et al., 2006). Interactive robots, however, have never been developed in order to interact with birds but it is possible that an interactive bird robot could be considered as a social agent and lead to behaviour changes in interactive and learning contexts (PhD project of Alice Araguas, under the supervision of Sébastien Derégnaucourt). It could then be possible for example to reproduce the experiment on social learning by using robot demonstrators, allowing us to control for confounding factors that could influence the social learning.

In animals, video playback and robotics are increasingly used to manipulate individual behaviours and isolate stimuli that are relevant in a context of social interaction. Even though these techniques are still subject to certain limitations, they provide new perspectives in the animal behaviour research and especially in the study of vocal and social learning in birds.

d) Genetic analyses

Genetic analyses are often conducted in parallel with song dialect studies but at a smaller scale (Baker, 1975; Soha et al., 2004). Such analyses can inform us about factors that could influence the birds' vocal, sexual or social behaviour. In the context of this thesis, genetic analyses would have provided us information on the birds' filiations within each artificial colony. Extra-pair copulations can occur in the wild zebra finch (Griffith et al., 2010), but occur much more often in domesticated birds (Birkhead et al., 1988, 1989, 1995). Thus, the foster father is not necessarily the genetic father. By crossing the results of genetic analyses with the social observations conducted during the sensitive phase of song learning, it would have been possible to identify from which birds each pupil preferentially learned his song: whether the pupil's song had more similar specificities with the biological father's song, the foster father's song, the brothers' song or the song of unrelated males. This could have informed us about the patterns of song learning that could have influenced the emergence of the artificial song dialects. In addition, genetic analyses could have also been helpful in interpreting the results of the second study. Indeed, the parentage genetic analyses could have helped us determine whether some females had already successfully reproduced with males, a factor that could have influenced their song preference. From a more general point of view, genetic analyses could provide new insights in the understanding of song learning mechanisms in free-living birds.

e) Song dialects as a social marker

We investigated whether song dialects could play a role as a group signature in the zebra finch through a social learning task. Such a role of song dialects was not confirmed by our results. In future studies this hypothesis could be tested using different approaches. In the context of the social adaptation hypothesis (Payne, 1981), it would be interesting to test whether a male zebra finch originating from a colony singing a specific song dialect would integrate more readily in a group singing the same song dialect than in a group singing a different song dialect. This could be tackled in in semi-natural aviaries by assessing social interactions (either affiliative or agonistic) and by evaluating access of those newly integrated males to females.

If song dialects do constitute a group signature in the zebra finch, this could have implications in group cohesion and cooperation (Hausberger et al., 2008). Therefore, a cooperation task could be a good way of addressing this issue in the zebra finch. Birds including finches can be trained to cooperate to get a food reward (St Pierre et al., 2009), so it should be possible to test whether zebra finches would be more likely to cooperate with birds singing the same song dialect than with a bird singing a different one.

Such experimentations would allow understanding the role of song dialects in zebra finches but in a more general way, they could be applied to other songbird species exhibiting song dialects in order to study whether vocal sharing could facilitate cooperation in birds.

f) Song learning as an indicator of personality and cognitive skills

In songbirds, it has recently been proposed that song traits could serve both as an indicator of personality (Garamszegi et al., 2008) and of cognitive abilities (Boogert et al., 2008). Additionally, it has been suggested that early social experience can affect personality traits in songbirds (Naguib et al., 2011), and that early nutritional conditions (Brust et al., 2014),

as well as some personality traits (Brust et al., 2013) could be correlated to the bird's performance in a cognitive task. So far results concerning the associations between aspects of adult song and cognitive abilities have been mixed, but some authors suggest that song learning is in itself a challenging cognitive task and that the accuracy with which songs are learned could constitute an indicator of cognitive abilities (Peters et al., 2014). However, to my knowledge, no published study has compared cognitive abilities in oscine songbirds raised in a controlled environment during the song production learning process. Preliminary results of studies conducted during my master's thesis on birds originating from our artificial colonies suggest that there is no correlation between song learning and success to solve a cognitive task in male zebra finches. These unpublished results also reveal difficulties in measuring personality traits using methods established for this species (cf. Brust et al., 2013; David et al., 2011, 2012): we obtained low repeatability for all personality traits measured. However, we did not take into account all possible parameters of song learning and further analysis are needed to conclude on the existence of a link between song learning and cognitive abilities in the zebra finch. More studies on oscine songbirds raised in a controlled laboratory environment should focus on this topic, because knowing whether such a relationship exists would represent a step further in understanding the dynamics of birdsong evolution.

g) Modeling the cultural evolution of birdsong

Modelling can be a good way of assessing the evolution of biological or behavioural traits and it has already been used to study the evolution of cultural traits. Language learning and evolution are the subject of intense attempts of modeling (Niyogi, 2006; Nowak et al., 2002). For example, different learning algorithms may have different evolutionary consequences (Niyogi, 2006). Such models of language learning and evolution that take into account the developmental aspect of the language acquisition process can be adapted to

birdsong learning and evolution. For example, in their study, Fehér and collaborators (2009) used two different experimental designs to assess the evolution of song starting from an isolated individual: a tutoring lineages design in which one isolated bird served as a tutor for a pupil, which himself became a tutor at adulthood, and so on; and an isolate colony setting in which one isolated tutor became the founder of an artificial colony, allowing pupils to have a richer social structure than in the first experimental design. In their study, they discuss their results using two models, each one reproducing one of the two experimental designs. Another example of birdsong evolution modelling is the one proposed by Lachlan and colleagues (2016) when studying the formation of vocal cultural traditions in the zebra finch. They conducted simulation models of cultural evolution using different song learning error rates and showed that cultural song divergence between populations would require very low error rates in the zebra finch syllable learning. However, such low error rates were not confirmed empirically (Lachlan et al., 2016). In another study, Lachlan and collaborators (2018) wondered what level of precision and what strategies in song learning could allow the rise of stable traditions, and addressed these issues using models of birdsong cultural evolution. Their simulations were based on song recordings of swamp sparrows and showed that a precise song learning combined to a conformist bias could allow syllable types to persist for hundreds of years, demonstrating extremely stable song traditions (Lachlan et al., 2018).

These examples show that cultural evolutionary models of song learning have been proven useful to understand the cultural evolution of birdsong. One logical consequence of this PhD project would be to model the cultural evolution of song within each of the three colonies. Based on the data that we accumulated, modelling would make it possible to investigate whether such artificial dialects would either remain stable over long periods of time, or quickly diverge and disappear, and which aspects of song production (song bout, motif, syllables or elements) and learning (such as faithful song imitation, learning errors or mutation) could

influence their evolution. Even if modelling appears as a very appealing and promising way of assessing cultural evolution of birdsong by comparing it also with genetic evolution, by itself it could probably not explain entirely how birdsong (or even human languages) can evolve. Instead, parallel analyses using mathematical models, computer simulations, empirical data and controlled experiments are required for a larger understanding of the cultural evolution of birdsong.

h) Understanding the origins and evolution of human speech using songbirds and other nonhuman animal models

With the extensive work on vocal learning and vocal culture in birdsong, more and more authors suggest that parallels can be drawn with the acquisition and evolution of human speech. In this context, this thesis work together with other studies on birdsong evolution, could contribute to a better understanding of the dynamics of cultural evolution of communication signals in humans and nonhuman animals.

According to some authors, spoken language is a faculty composed of multiple component traits, some that can be found in a broad range of species, and some that are specialized to few nonhuman animal species or only to humans (Jarvis, 2019). One component is auditory learning, i.e. "the ability to learn and remember novel sound associations" (Petkov & Jarvis, 2012). This component can be found in dogs that can be trained to associate objects to sounds of spoken names and then retrieve the correct named objects or a novel object (Kaminski et al., 2004). Another component of spoken language is vocal usage learning, i.e. "the ability to learn to produce innate or learned sounds in unfamiliar contexts" (Petkov & Jarvis, 2012). This ability can be found in chickens (*Gallus gallus domesticus*) or vervet monkeys in which juveniles learn the context of call production or behavioural response to conspecific calls through social experience (Seyfarth et al., 1980; Evans et al., 1993; Snowdon,

2009). Syntax is also considered as one component of human speech. However, it can arise for example in the vocalisations of Japanese tits (*Parus minor*) (Suzuki et al., 2019; but see Bolhuis et al., 2018), and it has been demonstrated that several bird species were able of grammatical rule discrimination and/or learning (ten Cate, 2014, 2018; Chen et al., 2015; Gentner et al., 2006; van Heijningen et al., 2013; Spierings & ten Cate, 2016). Such components could be continuous among species but more advanced in humans (Fitch, 2017; Jarvis, 2019), whereas other components such as vocal production learning would be rarer in animal species (but notably present in oscine songbirds) and extremely advanced in humans (Jarvis, 2019). However, evidences of artificial grammar learning in songbirds have been questions by recent studies (Beckers et al., 2017; Bolhuis et al., 2018). For example, Beckers and collaborators (2017) review stimulus designs of studies suggesting that their results demonstrate a form of sequence rule learning. They identify non salient biases in such studies, therefore reducing the strength of grammatical interpretations (Beckers et al., 2017). Other authors also criticise experimental findings on songbird syntax (Bolhuis et al., 2018). Even though they do not deny that some important behavioural and neural parallels exist in auditory and vocal imitation learning between infants and songbirds, they argue that there is so far no clear evidence that songbirds associate meaning with sounds, as humans do (Bolhuis et al., 2018). Such criticisms challenge the notion of similarities between birdsong and human speech.

When investigating vocal learning in human and nonhuman animals, it has often been assumed that species either do or do not have the ability of vocal production learning: either they are "vocal learners" or they are not. More recently, it has been proposed that vocal learning could be a continuum between species rather than a binary categorical distinction (Arriaga & Jarvis, 2013; Petkov & Jarvis, 2012). In this continuum, different species have different degrees of vocal learning that evolve in a stepwise manner: from 1) vocal non-learners, and 2) limited vocal learners such as vervet monkeys (Seyfarth & Cheney, 1986) or even mice (*Mus*

musculus), that make acoustical changes to innate ultrasonic vocalisations (Arriaga & Jarvis, 2013); to 3) complex vocal learners (songbirds), and 4) high vocal learner (humans) (Petkov & Jarvis, 2012). Additionally, this hypothesis of a continuum of vocal learning specifies that "the hierarchically higher the vocal-learning category is, the fewer species are observed in this category" (Petkov & Jarvis, 2012).

Finally, hypotheses about cognitive evolution suggest that, in order to support enhanced vocal communication perception or production learning, complex vocal learners such as humans and songbirds have improved cognitive abilities (e.g. in learning, attention and memory; Petkov & Jarvis, 2012). In this context, it is the capacities of cognitive systems that limit the level of sensory or vocal learning that an animal can express. This hypothesis is supported by several data showing for example that some vocal learners (e.g. elephants, dolphin and birds capable of vocal learning) have more advanced cognitive behaviours than humans' close relatives (Emery & Clayton, 2009, cited in: Petkov & Jarvis, 2012) such as monkeys, in which some researchers have showed a reduced capacity for auditory recognition memory (Fritz et al., 2005). Additionally, some researchers studying songbirds hypothesised that a male's song complexity might provide an indicator of his general cognitive abilities and quality as a mate (Boogert et al., 2008; Catchpole, 1996; DeVoogd, 2004; Nowicki et al., 2000; Nowicki & Searcy, 2011; Templeton et al., 2014). As mentioned before, studies focusing on the link between cognitive abilities and adult song have provided mixed results. Moreover, the hypothesis of a link between song learning and other cognitive abilities was recently questioned by the very research team who originally formulated it (DuBois et al., 2018; Searcy & Nowicki, 2019), suggesting that song learning is an autonomous cognitive module rather than a component of domain-general cognition (Searcy & Nowicki, 2019). An opposite point of view to this cognitive evolution hypothesis could then be considered: that speech and song abilities are supported by neurobiological substrates that are considerably specialised for vocal

production learning (Petkov & Jarvis, 2012). Similarly, some linguists suggested a language modularity that would be independent of other cognitive abilities (Carruthers & Chamberlain, 2000). In the case of songbirds, such a point of view would indicate that the song control system would be independent from other neuronal pathways implicated in cognitive abilities, explaining why poor song learners or males with less complex songs would not necessarily be worse in solving cognitive tasks. To conclude on whether vocal learning originated as a by-product of advanced cognitive abilities or whether the modularity of vocal learning evolved independently from such abilities, more research investigating cognitive abilities of vocal learners and non-learners are required.

These new ideas of how the human language originated and evolved do validate the songbird as a relevant model to study such aspects of human speech, in view of its proximity to humans in the expressed components of vocal learning and in its place on the vocal learning continuum. However, they also emphasize that studies should not only focus on the few species that are thought to have communication abilities most comparable to humans, but rather adopt a broader comparative approach by obtaining information across different animal taxa.

II) CONCLUSION

This thesis provides new insights on the process of cultural evolution of birdsong in controlled laboratory conditions. We assessed the potential functional significance of song cultures, that is, their bearing on whether females prefer their natal song dialect over a foreign one and whether such song dialects could play a role as a group signature, influencing the birds' social learning in the context of food choice. The main finding of this thesis validates the existence of a tension between birdsong learning and birdsong cultural evolution: on one hand, song learning can be robust and reliable, but on the other hand, song learning cannot be perfect or else birdsong would not change over time. More importantly, it revealed that different parts

of the song structure could evolved independently, with changes that could potentially be guided by opposed social forces. One thing we know for sure with our findings is that song dialects do matter to females, even if we could not fully understand the nature of this importance. The last experiment tested whether song dialects could have an importance in social learning in this species. This experiment revealed the difficulties of unravelling the effects of song dialects and those of other behavioural traits. In addition to conduct further analyses and use new methods on the existing data, many more studies still need to be done on zebra finches but also on other songbird species raised under laboratory conditions, in order to fully understand the dynamics of the cultural evolution of communication signals. Finally, this thesis work could potentially contribute to the field of research that investigates the origins and evolution of human language by participating to the concerted efforts in accumulating data from many nonhuman animal species.

References

REFERENCES

Adret, P. (1993a). Operant conditioning, song learning and imprinting to taped song in the zebra finch. *Animal Behaviour*, *46*(1), 149–159.

Adret, P. (1993b). Vocal learning induced with operant techniques: An overview. *Netherlands Journal of Zoology*, *43*, 125–125.

Akçay, Ç., Tom, M. E., Campbell, S. E., & Beecher, M. D. (2013). Song type matching is an honest early threat signal in a hierarchical animal communication system. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1756), 20122517. https://doi.org/10.1098/rspb.2012.2517

Akçay, Ç., Campbell, S. E., Reed, V. A., & Beecher, M. D. (2014). Song sparrows do not learn more songs from aggressive tutors. *Animal Behaviour*, *94*, 151–159. https://doi.org/10.1016/j.anbehav.2014.06.003

Alem, S., Perry, C. J., Zhu, X., Loukola, O. J., Ingraham, T., Søvik, E., & Chittka, L. (2016). Associative Mechanisms Allow for Social Learning and Cultural Transmission of String Pulling in an Insect. *PLOS Biology*, *14*(10), e1002564. https://doi.org/10.1371/journal.pbio.1002564

Alvard, M. S. (2003). The adaptive nature of culture. *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(3), 136–149. https://doi.org/10.1002/evan.10109

Amador, A., Perl, Y. S., Mindlin, G. B., & Margoliash, D. (2013). Elemental gesture dynamics are encoded by song premotor cortical neurons. *Nature*, *495*(7439), 59–64. https://doi.org/10.1038/nature11967

Amy, M., Monbureau, M., Durand, C., Gomez, D., Théry, M., & Leboucher, G. (2008). Female canary mate preferences: Differential use of information from two types of male–male interaction. *Animal Behaviour*, *76*(3), 971–982. https://doi.org/10.1016/j.anbehav.2008.03.023

Andalman, A. S., & Fee, M. S. (2009). A basal ganglia-forebrain circuit in the songbird biases motor output to avoid vocal errors. *Proceedings of the National Academy of Sciences*, *106*(30), 12518–12523. https://doi.org/10.1073/pnas.0903214106

Andrew, R. J. (1962). Evolution of Intelligence and Vocal Mimicking. *Science*, *137*(3530), 585–589.

Anisimov, V. N., Herbst, J. A., Abramchuk, A. N., Latanov, A. V., Hahnloser, R. H., & Vyssotski, A.

L. (2014). Reconstruction of vocal interactions in a group of small songbirds. *Nature Methods*, *11*(11), 1135–1137.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). *Counting conformity: Evaluating the units of information in frequency-dependent social learning*. https://doi.org/10.1016/j.anbehav.2015.09.015

Aplin, L. M. (2019). Culture and cultural evolution in birds: A review of the evidence. *Animal Behaviour*, *147*, 179–187. https://doi.org/10.1016/j.anbehav.2018.05.001

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*(7540), 538–541.

Aplin, L. M., Sheldon, B. C., & McElreath, R. (2017). Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. *Proceedings of the National Academy of Sciences*, *114*(30), 7830–7837. https://doi.org/10.1073/pnas.1621067114

Araki, M., Bandi, M. M., & Yazaki-Sugiyama, Y. (2016). Mind the gap: Neural coding of species identity in birdsong prosody. *Science*, *354*(6317), 1282–1287. https://doi.org/10.1126/science.aah6799

Armstrong, E. A. (1955). The Wren. London: Collins.

Arriaga, G., & Jarvis, E. D. (2013). Mouse vocal communication system: Are ultrasounds learned or innate? *Brain and Language*, *124*(1), 96–116. https://doi.org/10.1016/j.bandl.2012.10.002

Auld, H. L., Punzalan, D., Godin, J. G. J., & Rundle, H. D. (2009). Do female fruit flies (*Drosophila serrata*) copy the mate choice of others? *Behavioural Processes*, *82*(1), 78–80. https://doi.org/10.1016/j.beproc.2009.03.004

Avital, E., & Jablonka, E. (2000). *Animal Traditions: Behavioural Inheritance in Evolution*. https://doi.org/10.1017/CBO9780511542251

Baker, A. J., & Jenkins, P. F. (1987). Founder effect and cultural evolution of songs in an isolated population of chaffinches, *Fringilla coelebs,* in the Chatham Islands. *Animal Behaviour*, *35*(6), 1793–1803. https://doi.org/10.1016/S0003-3472(87)80072-6

Baker, M. C. (1996). Depauperate meme pool of vocal signals in an island population of singing

honeyeaters. *Animal Behaviour*, *51*(4), 853–858. https://doi.org/10.1006/anbe.1996.0089

Baker, M. C. (2000). Cultural Diversification in the Flight Call of the Ringneck Parrot in Western Australia. *The Condor*, *102*(4), 905–910. https://doi.org/10.1093/condor/102.4.905

Baker, M. C., Baker, M. S. A., & Tilghman, L. M. (2006). Differing effects of isolation on evolution of bird songs: Examples from an island-mainland comparison of three species. *Biological Journal of the Linnean Society*, *89*(2), 331–342. https://doi.org/10.1111/j.1095-8312.2006.00677.x

Baker, M. C. (1975). Song dialects and genetic differences in white-crowned sparrows (*Zonotrichia leucophrys*). *Evolution*, *29*(2), 226–241.

Baker, M. C. (1983). The behavioral response of female Nuttall's White-crowned Sparrows to male song of natal and alien dialects. *Behavioral Ecology and Sociobiology*, *12*(4), 309–315. https://doi.org/10.1007/BF00302898

Baker, M. C., & Cunningham, M. A. (1985). The Biology of Bird-Song Dialects. *Behavioral and Brain Sciences*, *8*(1), 85–100. https://doi.org/10.1017/S0140525X00019750

Baker, M. C., Spitler-Nabors, K. J., & Bradley, D. C. (1981). Early Experience Determines Song Dialect Responsiveness of Female Sparrows. *Science*, *214*(4522), 819–821. https://doi.org/10.1126/science.214.4522.819

Baker, M. C., Spitler-Nabors, K. J., & Bradley, D. C. (1982). The response of female Mountain White-crowned Sparrows to songs from their natal dialect and an alien dialect. *Behavioral Ecology and Sociobiology*, *10*(3), 175–179. https://doi.org/10.1007/BF00299682

Baptista, L. F., & Trail, P. W. (1992). The Role of Song in the Evolution of Passerine Diversity. *Systematic Biology*, *41*(2), 242–247. https://doi.org/10.2307/2992524

Beckers, G. J. L., Berwick, R. C., Okanoya, K., & Bolhuis, J. J. (2017). What do animals learn in artificial grammar studies? *Neuroscience & Biobehavioral Reviews*, *81*, 238–246. https://doi.org/10.1016/j.neubiorev.2016.12.021

Beecher, M. D., & Burt, J. M. (2004). The Role of Social Interaction in Bird Song Learning. *Current Directions in Psychological Science*, *13*(6), 224–228. https://doi.org/10.1111/j.0963-7214.2004.00313.x

Béguin, N., Leboucher, G., & Kreutzer, M. L. (1998). Sexual Preferences for Mate Song in Female

Canaries (*Serinus Canaria*). *Behaviour*, *135*(8), 1185–1196. https://doi.org/10.1163/156853998792913500

Belzner, S., Voigt, C., Catchpole, C. K., & Leitner, S. (2009). Song learning in domesticated canaries in a restricted acoustic environment. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 2881–2886. https://doi.org/10.1098/rspb.2009.0669

Benskin, C. M. H., Mann, N. I., Lachlan, R. F., & Slater, P. J. B. (2002). Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, *64*(5), 823–828. https://doi.org/10.1006/anbe.2002.2005

Birkhead, T. R., Burke, T., Zann, R., Hunter, F. M., & Krupa, A. P. (1990). Extra-pair paternity and intraspecific brood parasitism in wild zebra finches *Taeniopygia guttata*, revealed by DNA fingerprinting. *Behavioral Ecology and Sociobiology*, *27*(5), 315–324. https://doi.org/10.1007/BF00164002

Birkhead, T. R., Fletcher, F., Pellatt, E. J., & Staples, A. (1995). Ejaculate quality and the success of extra-pair copulations in the zebra finch. *Nature*, *377*(6548), 422–423.

Birkhead, T. R., Hunter, F. M., & Pellatt, J. E. (1989). Sperm competition in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, *38*(6), 935–950. https://doi.org/10.1016/S0003-3472(89)80135-6

Birkhead, T. R., Pellatt, J., & Hunter, F. M. (1988). Extra-pair copulation and sperm competition in the zebra finch. *Nature*, *334*(6177), 60.

Bluff, L. A., Kacelnik, A., & Rutz, C. (2010). Vocal culture in New Caledonian crows *Corvus moneduloides*. *Biological Journal of the Linnean Society*, *101*(4), 767–776. https://doi.org/10.1111/j.1095-8312.2010.01527.x

Bluff, L. A., Troscianko, J., Weir, A. A. S., Kacelnik, A., & Rutz, C. (2010). Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1686), 1377–1385. https://doi.org/10.1098/rspb.2009.1953

Boesch, C. (1993). Towards a new image of culture in wild chimpanzees? *Behavioral and Brain Sciences*, *16*(3), 514–515. https://doi.org/10.1017/S0140525X00031277

Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(2), 82–91. https://doi.org/10.1002/evan.10106

REFERENCES

Bolhuis, J. J., Beckers, G. J. L., Huybregts, M. A. C., Berwick, R. C., & Everaert, M. B. H. (2018). Meaningful syntactic structure in songbird vocalizations? *PLOS Biology*, *16*(6), e2005157. https://doi.org/10.1371/journal.pbio.2005157

Bolhuis, J. J., & Gahr, M. (2006). Neural mechanisms of birdsong memory. *Nature Reviews Neuroscience*, *7*(5), 347–357. https://doi.org/10.1038/nrn1904

Bolhuis, J. J., Okanoya, K., & Scharff, C. (2010). Twitter evolution: Converging mechanisms in birdsong and human speech. *Nature Reviews Neuroscience*, *11*(11), 747–759. https://doi.org/10.1038/nrn2931

Boogert, N. J., Farine, D. R., & Spencer, K. A. (2014). Developmental stress predicts social network position. *Biology Letters*, *10*(10), 20140561. https://doi.org/10.1098/rsbl.2014.0561

Boogert, N. J., Giraldeau, L. A., & Lefebvre, L. (2008). Song complexity correlates with learning ability in zebra finch males. *Animal Behaviour*, *76*(5), 1735–1741.

Boucaud, I. C. A., Mariette, M. M., Villain, A. S., & Vignal, C. (2016). Vocal negotiation over parental care? Acoustic communication at the nest predicts partners' incubation share. *Biological Journal of the Linnean Society*, *117*(2), 322–336. https://doi.org/10.1111/bij.12705

Boucaud, I. C. A., Perez, E. C., Ramos, L. S., Griffith, S. C., & Vignal, C. (2017). Acoustic communication in zebra finches signals when mates will take turns with parental duties. *Behavioral Ecology*, *28*(3), 645–656. https://doi.org/10.1093/beheco/arw189

Boughman, J. W. (1997). Greater spear-nosed bats give group-distinctive calls. *Behavioral Ecology and Sociobiology*, *40*(1), 61–70. https://doi.org/10.1007/s002650050316

Boughman, J. W. (1998). Vocal learning by greater spear–nosed bats. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1392), 227–233. https://doi.org/10.1098/rspb.1998.0286

Bowman, R. I. (1979). Adaptive morphology of song dialects in Darwin's finches. *Journal Für Ornithologie*, *120*(4), 353–389. https://doi.org/10.1007/BF01642911

Bowman, R. I. (1983). The evolution of song in Darwin's finches. *In: Patterns of evolution in Galapagos organisms (ed. R. I. Bowman, M. Berson & A. E. Leviton), pp. 237–538.San Francisco, CA: Pacific Division of the American Association for the Advancement of Science.*

REFERENCES

Boyd, R., & Richerson, P. J. (1985). *Culture and the Evolutionary Process*. University of Chicago Press.

Boyd, R., & Richerson, P. J. (1988). *In: Social Learning in Animals. Psychological and Biological Perspectives (Zentall, T., & Galef Jr, B. G., eds.) 29–48 (Lawrence Erlbaum Associates, Publishers, Hillsdale, New Jersey, Hove and London, 1988).*

Bradbury, J. W., Cortopassi, K. A., Clemmons, J. R., & Kroodsma, D. (2001). Geographical Variation in the Contact Calls of Orange-Fronted Parakeets. *The Auk*, *118*(4), 958–972. https://doi.org/10.1093/auk/118.4.958

Brainard, M. S., & Doupe, A. J. (2002). What songbirds teach us about learning. *Nature*, *417*(6886), 351–358.

Bridges, A. D., & Chittka, L. (2019). Animal Behaviour: Conformity and the Beginnings of Culture in an Insect. *Current Biology*, *29*(5), R167–R169. https://doi.org/10.1016/j.cub.2019.01.023

Briefer, E., Aubin, T., Lehongre, K., & Rybak, F. (2008). How to identify dear enemies: The group signature in the complex song of the skylark *Alauda arvensis*. *Journal of Experimental Biology*, *211*(3), 317–326. https://doi.org/10.1242/jeb.013359

Brooks, R. (1998). The importance of mate copying and cultural inheritance of mating preferences. *Trends in Ecology & Evolution*, *13*(2), 45–46.

Brumm, H., Zollinger, S. A., Niemelä, P. T., & Sprau, P. (2017). Measurement artefacts lead to false positives in the study of birdsong in noise. *Methods in Ecology and Evolution*, *8*(11), 1617–1625. https://doi.org/10.1111/2041-210X.12766

Bruner, J. S. (1981). The social context of language acquisition. *Language & Communication*, *1*(2–3), 155–178. https://doi.org/10.1016/0271-5309(81)90010-0

Brust, V., Krüger, O., Naguib, M., & Krause, E. T. (2014). Lifelong consequences of early nutritional conditions on learning performance in zebra finches (*Taeniopygia guttata)*. *Behavioural Processes*, *103*, 320–326. https://doi.org/10.1016/j.beproc.2014.01.019

Brust, V., Wuerz, Y., & Krüger, O. (2013). Behavioural flexibility and personality in zebra finches. *Ethology*, *119*(7), 559–569.

Byers, B. E., Belinsky, K. L., & Bentley, R. A. (2010). Independent Cultural Evolution of Two Song Traditions in the Chestnut-Sided Warbler. *The American Naturalist*, *176*(4), 476–489.

https://doi.org/10.1086/656268

Carouso-Peck, S., & Goldstein, M. H. (2019). Female Social Feedback Reveals Non-imitative Mechanisms of Vocal Learning in Zebra Finches. *Current Biology*. https://doi.org/10.1016/j.cub.2018.12.026

Carruthers, P., & Chamberlain, A. (2000). *Evolution and the human mind: Modularity, language and meta-cognition*.

Catchpole, C. K., & Slater, P. J. B. (2008). Bird Song: Biological Themes and Variations. *Cambridge University, Cambridge*.

Catchpole, C. K. (1996). Song and female choice: Good genes and big brains? *Trends in Ecology & Evolution*, *11*(9), 358–360. https://doi.org/10.1016/0169-5347(96)30042-6

Chaiken, M., Böhner, J., & Marler, P. (1994). Repertoire Turnover and the Timing of Song Acquisition in European Starlings. *Behaviour*, *128*(1–2), 25–39. https://doi.org/10.1163/156853994X00037

Chen, J., van Rossum, D., & ten Cate, C. (2015). Artificial grammar learning in zebra finches and human adults: XYX versus XXY. *Animal Cognition*, *18*(1), 151–164. https://doi.org/10.1007/s10071-014-0786-4

Chen, Y., Matheson, L. E., & Sakata, J. T. (2016). Mechanisms underlying the social enhancement of vocal learning in songbirds. *Proceedings of the National Academy of Sciences*, 201522306.

Claidière, N., Smith, K., Kirby, S., & Fagot, J. (2014). Cultural evolution of systematically structured behaviour in a non-human primate. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797), 20141541. https://doi.org/10.1098/rspb.2014.1541

Clayton, D. A. (1978). Socially Facilitated Behavior. *The Quarterly Review of Biology*, *53*(4), 373–392. https://doi.org/10.1086/410789

Clayton, N. S. (1987). Song tutor choice in zebra finches. *Animal Behaviour*, *35*(3), 714–721. https://doi.org/10.1016/S0003-3472(87)80107-0

Clayton, N. S. (1988). Song discrimination learning in zebra finches. *Animal Behaviour*, *36*(4), 1016–1024. https://doi.org/10.1016/S0003-3472(88)80061-7

Clayton, N. S. (1990). Subspecies recognition and song learning in zebra finches. *Animal Behaviour*, *40*(6), 1009–1017. https://doi.org/10.1016/S0003-3472(05)80169-1

Cornish, H., Smith, K., & Kirby, S. (2013). Systems from sequences: An iterated learning account of the emergence of systematic structure in a non-linguistic task. *Proceedings of the Annual Meeting of the Cognitive Science Society*, *35*.

Cramp, S. (1988). The Birds of the Western Palearctic. *Vol. 5. Oxford: Oxford University Press.*

Cynx, J., & Nottebohm, F. (1992). Role of gender, season, and familiarity in discrimination of conspecific song by zebra finches (*Taeniopygia guttata*). *Proceedings of the National Academy of Sciences*, *89*(4), 1368–1371.

Danchin, E., Blanchet, S., Mery, F., & Wagner, R. H. (2010). Do invertebrates have culture? *Communicative & Integrative Biology*, *3*(4), 303–305. https://doi.org/10.4161/cib.3.4.11970

Danchin, E., Nöbel, S., Pocheville, A., Dagaeff, A. C., Demay, L., Alphand, M., Ranty-Roby, S., Renssen, L., Monier, M., Gazagne, E., Allain, M., & Isabel, G. (2018). Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science*, *362*(6418), 1025–1030. https://doi.org/10.1126/science.aat1590

Danchin, E., & Wagner, R. H. (2008). Cultural evolution. *Behavioural Ecology: An Evolutionary Perspective on Behaviour*, 693–726.

Danchin, E., & Wagner, R. H. (2010). Inclusive heritability: Combining genetic and non-genetic information to study animal behavior and culture. *Oikos*, *119*(2), 210–218. https://doi.org/10.1111/j.1600-0706.2009.17640.x

David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, *81*(1), 219–224.

David, M., Auclair, Y., & Cézilly, F. (2012). Assessing Short-and Long-Term Repeatability and Stability of Personality in Captive Zebra Finches Using Longitudinal Data. *Ethology*, *118*(10), 932–942.

Davidson, S. M., & Wilkinson, G. S. (2002). Geographic and Individual Variation in Vocalizations by Male *Saccopteryx Bilineata* (Chiroptera: Emballonuridae). *Journal of Mammalogy*, *83*(2), 526–535.

de Waal, F. B. M. (1999). Cultural primatology comes of age. *Nature*, *399*(6737), 635–636. https://doi.org/10.1038/21310

de Waal, F. B. M. (2001). The ape and the sushi master. *London: Penguin*

Dell, A. I., Bender, J. A., Branson, K., Couzin, I. D., de Polavieja, G. G., Noldus, L. P. J. J., Pérez-Escudero, A., Perona, P., Straw, A.D., Wikelski, M., & Brose, U. (2014). Automated image-based tracking and its application in ecology. *Trends in Ecology & Evolution*, *29*(7), 417–428. https://doi.org/10.1016/j.tree.2014.05.004

Derégnaucourt, S. (2011). Birdsong learning in the laboratory, with especial reference to the song of the Zebra Finch (Taeniopygia guttata). *Interaction Studies*, *12*(2), 324–350. https://doi.org/10.1075/is.12.2.07der

Derégnaucourt, S., & Gahr, M. (2013). Horizontal transmission of the father's song in the zebra finch (*Taeniopygia guttata*). *Biology Letters*, *9*(4), 20130247. https://doi.org/10.1098/rsbl.2013.0247

Derégnaucourt, S., Mitra, P. P., Fehér, O., Pytte, C., & Tchernichovski, O. (2005). How sleep affects the developmental learning of bird song. *Nature*, *433*(7027), 710–716. https://doi.org/10.1038/nature03275

Derégnaucourt, S., Poirier, C., Van der Kant, A., Van der Linden, A., & Gahr, M. (2013). Comparisons of different methods to train a young zebra finch (*Taeniopygia guttata*) to learn a song. *Journal of Physiology-Paris*, *107*(3), 210–218.

Derégnaucourt, S., Saar, S., & Gahr, M. (2009). Dynamics of crowing development in the domestic Japanese quail (*Coturnix coturnix japonica*). *Proceedings of the Royal Society B: Biological Sciences*, *276*(1665), 2153–2162. https://doi.org/10.1098/rspb.2009.0016

Derryberry, E. P. (2007). Evolution of Bird Song Affects Signal Efficacy: An Experimental Test Using Historical and Current Signals. *Evolution*, *61*(8), 1938–1945. https://doi.org/10.1111/j.1558-5646.2007.00154.x

Derryberry, E. P. (2011). Male response to historical and geographical variation in bird song. *Biology Letters*, *7*(1), 57–59.

Derryberry, E. P., Seddon, N., Claramunt, S., Tobias, J. A., Baker, A., Aleixo, A., & Brumfield, R. T. (2012). Correlated Evolution of Beak Morphology and Song in the Neotropical Woodcreeper Radiation. *Evolution*, *66*(9), 2784–2797. https://doi.org/10.1111/j.1558-5646.2012.01642.x

Derryberry, E. P. (2009). Ecology Shapes Birdsong Evolution: Variation in Morphology and Habitat

Explains Variation in White-Crowned Sparrow Song. *The American Naturalist*, *174*(1), 24–33. https://doi.org/10.1086/599298

Deshpande, M., Pirlepesov, F., & Lints, T. (2014). Rapid encoding of an internal model for imitative learning. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1781), 20132630. https://doi.org/10.1098/rspb.2013.2630

DeVoogd, T. J. (2004). Neural Constraints on the Complexity of Avian Song. *Brain, Behavior and Evolution*, *63*(4), 221–232. https://doi.org/10.1159/000076783

Diamond, J. (1986). Animal art: Variation in bower decorating style among male bowerbirds *Amblyornis inornatus*. *Proceedings of the National Academy of Sciences*, *83*(9), 3042–3046. https://doi.org/10.1073/pnas.83.9.3042

Diamond, J. (1987). Bower Building and Decoration by the Bowerbird *Amblyornis inornatus*. *Ethology*, *74*(3), 177–204. https://doi.org/10.1111/j.1439-0310.1987.tb00932.x

Diamond, J. M. (1982). Evolution of bowerbirds' bowers: Animal origins of the aesthetic sense. *Nature*, *297*(5862), 99–102. https://doi.org/10.1038/297099a0

Doupe, A. J., & Kuhl, P. K. (1999). Birdsong and human speech: Common Themes and Mechanisms. *Annual Review of Neuroscience*, *22*(1), 567–631. https://doi.org/10.1146/annurev.neuro.22.1.567

Draganoiu, T. I., Moreau, A., Ravaux, L., Bonckaert, W., & Mathevon, N. (2014). Song stability and neighbour recognition in a migratory songbird, the black redstart. *Behaviour*, *151*(4), 435–453. https://doi.org/10.1163/1568539X-00003129

DuBois, A. L., Nowicki, S., Peters, S., Rivera-Cáceres, K. D., & Searcy, W. A. (2018). Song is not a reliable signal of general cognitive ability in a songbird. *Animal Behaviour*, *137*, 205–213.

Durham, W. H. (1991). *Coevolution: Genes, culture, and human diversity*. Stanford University Press.

Eales, L. A. (1989). The influences of visual and vocal interaction on song learning in zebra finches. *Animal Behaviour*, *37*, 507–508.

Edwards, S. V., Kingan, S. B., Calkins, J. D., Balakrishnan, C. N., Jennings, W. B., Swanson, W. J., & Sorenson, M. D. (2005). Speciation in birds: Genes, geography, and sexual selection. *Proceedings of the National Academy of Sciences*, *102*, 6550–6557.

https://doi.org/10.1073/pnas.0501846102

Elie, J. E., Soula, H. A., Mathevon, N., & Vignal, C. (2011). Dynamics of communal vocalizations in a social songbird, the zebra finch (*Taeniopygia guttata*). *The Journal of the Acoustical Society of America*, *129*(6), 4037–4046. https://doi.org/10.1121/1.3570959

Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: Functional reference in an avian vocal system. *Animal Behaviour*, *46*(1), 23–38. https://doi.org/10.1006/anbe.1993.1158

Fayet, A. L., Tobias, J. A., Hintzen, R. E., & Seddon, N. (2014). Immigration and dispersal are key determinants of cultural diversity in a songbird population. *Behavioral Ecology*, *25*(4), 744–753. https://doi.org/10.1093/beheco/aru047

Feekes, F. (1977). Colony-specific song in *Cacicus cela* (Icteridae, Aves): The password hypothesis. *Ardea*, *65*(3–4), 197–202.

Feher, O., Wang, H., Saar, S., Mitra, P. P., & Tchernichovski, O. (2009). De novo establishment of wild-type song culture in the zebra finch. *Nature*, *459*(7246), 564–568.

Fernald, A., & Kuhl, P. (1987). Acoustic determinants of infant preference for motherese speech. *Infant Behavior and Development*, *10*(3), 279–293. https://doi.org/10.1016/0163-6383(87)90017-8

Fisher, J., & Hinde, R. A. (1949). The opening of milk bottles by birds. *British Birds*, *42*, 347–357.

Fitch, W. T. (2017). Empirical approaches to the study of language evolution. *Psychonomic Bulletin & Review*, *24*(1), 3–33. https://doi.org/10.3758/s13423-017-1236-5

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, *69*(6), 1454–1483. https://doi.org/10.1139/z91-206

Franz, M., & Matthews, L. J. (2010). Social enhancement can create adaptive, arbitrary and maladaptive cultural traditions. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1698), 3363–3372. https://doi.org/10.1098/rspb.2010.0705

Freeberg, T. M. (1996). Assortative mating in captive cowbirds is predicted by social experience. *Animal Behaviour*, *52*(6), 1129–1142.

Freeberg, T. M. (1998). The cultural transmission of courtship patterns in cowbirds, *Molothrus ater*. *Animal Behaviour*, *56*(5), 1063–1073.

Freeberg, T. M. (2000). Culture and courtship in vertebrates: A review of social learning and transmission of courtship systems and mating patterns. *Behavioural Processes*, *51*(1), 177–192. https://doi.org/10.1016/S0376-6357(00)00127-3

Freeberg, T. M., Duncan, S. D., Kast, T. L., & Enstrom, D. A. (1999). Cultural influences on female mate choice: An experimental test in cowbirds, *Molothrus ater*. *Animal Behaviour*, *57*(2), 421–426.

Fritz, J., Mishkin, M., & Saunders, R. C. (2005). In search of an auditory engram. *Proceedings of the National Academy of Sciences*, *102*(26), 9359–9364. https://doi.org/10.1073/pnas.0503998102

Gadagkar, V., Puzerey, P. A., Chen, R., Baird-Daniel, E., Farhang, A. R., & Goldberg, J. H. (2016). Dopamine neurons encode performance error in singing birds. *Science*, *354*(6317), 1278–1282. https://doi.org/10.1126/science.aah6837

Galef, B. G. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In *Social learning: Psychological and biological perspectives* (pp. 3–28). Hillsdale, NJ, US: Lawrence Erlbaum Associates, Inc.

Galef, B. G. (1976). Social Transmission of Acquired Behavior: A Discussion of Tradition and Social Learning in Vertebrates. In J. S. Rosenblatt, R. A. Hinde, E. Shaw, & C. Beer (Eds.), *Advances in the Study of Behavior* (Vol. 6, pp. 77–100). https://doi.org/10.1016/S0065-3454(08)60082-0

Galef, B. G. (1992). The question of animal culture. *Human Nature*, *3*(2), 157–178. https://doi.org/10.1007/BF02692251

Galef, B. G. (2003). Social learning: promoter or inhibitor of innovation? *In: Reader SM, Laland KN, editors. Animal innovation. Oxford: Oxford University Press.*

Garamszegi, L. Z., Eens, M., & Török, J. (2008). Birds reveal their personality when singing. *PLoS One*, *3*(7), e2647.

Garamszegi, L. Z., Pavlova, D. Z., Eens, M., & Møller, A. P. (2007). The evolution of song in female birds in Europe. *Behavioral Ecology*, *18*(1), 86–96. https://doi.org/10.1093/beheco/arl047

García, N. C., Arrieta, R. S., Kopuchian, C., & Tubaro, P. L. (2015). Stability and change through time in the dialects of a Neotropical songbird, the Rufous-collared Sparrow. *Emu*, *115*(4), 309–316.

Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Hauser, N. D., Poole,

M. M., Robbins, J., & Noad, M. J. (2011). Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology*, *21*(8), 687–691.

Gaunt, S. L. L., Baptista, L. F., S¡nchez, J. E., & Hernandez, D. (1994). Song Learning as Evidenced from Song Sharing in Two Hummingbird Species (*Colibri Coruscans* and *C. Thalassinus*). *The Auk*, *111*(1), 87–103. https://doi.org/10.2307/4088508

Gentner, T. Q., Fenn, K. M., Margoliash, D., & Nusbaum, H. C. (2006). Recursive syntactic pattern learning by songbirds. *Nature*, *440*(7088), 1204–1207. https://doi.org/10.1038/nature04675

Gibson, R. M., Bradbury, J. W., & Vehrencamp, S. L. (1991). Mate choice in lekking sage grouse revisited: The roles of vocal display, female site fidelity, and copying. *Behavioral Ecology*, *2*(2), 165–180. https://doi.org/10.1093/beheco/2.2.165

Gill, L. F., Goymann, W., Ter Maat, A., & Gahr, M. (2015). Patterns of call communication between group-housed zebra finches change during the breeding cycle. *Elife*, *4*, e07770.

Gish, S. L., & Morton, E. S. (1981). Structural Adaptations to Local Habitat Acoustics in Carolina Wren Songs. *Zeitschrift Für Tierpsychologie*, *56*(1), 74–84. https://doi.org/10.1111/j.1439-0310.1981.tb01285.x

Goodall, J. (1973). Cultural elements in a chimpanzee community. *Precultural Primate Behavior*.

Goodfellow, D. J., & Slater, P. J. (1986). A model of bird song dialects. *Animal Behaviour*, *34*(5), 1579–1580. https://doi.org/10.1016/S0003-3472(86)80233-0

Griffith, B., Scott, J. M., Carpenter, J. W., & Reed, C. (1989). Translocation as a Species Conservation Tool: Status and Strategy. *Science*, *245*(4917), 477–480. https://doi.org/10.1126/science.245.4917.477

Griffith, S. C., Holleley, C. E., Mariette, M. M., Pryke, S. R., & Svedin, N. (2010). Low level of extrapair parentage in wild zebra finches. *Animal Behaviour*, *79*(2), 261–264. https://doi.org/10.1016/j.anbehav.2009.11.031

Guillette, L. M., & Healy, S. D. (2014). Mechanisms of copying behaviour in zebra finches. *Behavioural Processes*, *108*, 177–182. https://doi.org/10.1016/j.beproc.2014.10.011

Guillette, L. M., & Healy, S. D. (2017). The roles of vocal and visual interactions in social learning zebra finches: A video playback experiment. *Behavioural Processes*, *139*, 43–49.

https://doi.org/10.1016/j.beproc.2016.12.009

Guinet, C., & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology*, *73*(1), 27–33. https://doi.org/10.1139/z95-004

Gurney, M. E. (1982). Behavioral correlates of sexual differentiation in the zebra finch song system. *Brain Research*, *231*(1), 153–172. https://doi.org/10.1016/0006-8993(82)90015-4

Haesler, S., Rochefort, C., Georgi, B., Licznerski, P., Osten, P., & Scharff, C. (2007). Incomplete and Inaccurate Vocal Imitation after Knockdown of FoxP2 in Songbird Basal Ganglia Nucleus Area X. *PLOS Biology*, *5*(12), e321. https://doi.org/10.1371/journal.pbio.0050321

Hall, M. L., Kingma, S. A., & Peters, A. (2013). Male Songbird Indicates Body Size with Low-Pitched Advertising Songs. *PLoS One*, *8*(2), e56717. https://doi.org/10.1371/journal.pone.0056717

Handford, P. (1988). Trill rate dialects in the Rufous-collared Sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Canadian Journal of Zoology*, *66*(12), 2658–2670. https://doi.org/10.1139/z88-391

Hansen, P. (1979). Vocal learning: Its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Animal Behaviour*, *27*(4), 1270–1271. https://doi.org/10.1016/0003-3472(79)90073-3

Harbison, H., Nelson, D. A., & Hahn, T. P. (1999). Long-Term Persistence of Song Dialects in the Mountain White-Crowned Sparrow. *The Condor*, *101*(1), 133–148. https://doi.org/10.2307/1370454

Hart, P. J., Sebastián-González, E., Tanimoto, A., Thompson, A., Speetjens, T., Hopkins, M., & Atencio-Picado, M. (2018). Birdsong characteristics are related to fragment size in a neotropical forest. *Animal Behaviour*, *137*, 45–52. https://doi.org/10.1016/j.anbehav.2017.12.020

Hausberger, M., Bigot, E., & Clergeau, P. (2008). Dialect use in large assemblies: A study in European starling *Sturnus vulgaris* roosts. *Journal of Avian Biology*, *39*(6), 672–682.

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, *298*(5598), 1569–1579. https://doi.org/10.1126/science.298.5598.1569

Helfman, G. S., & Schultz, E. T. (1984). Social transmission of behavioural traditions in a coral reef fish. *Animal Behaviour*, *32*(2), 379–384. https://doi.org/10.1016/S0003-3472(84)80272-9

Henrich, J. (2001). Cultural transmission and the diffusion of innovations: Adoption dynamics indicate that biased cultural transmission is the predominate force in behavioral change. *American Anthropologist*, *103*(4), 992–1013.

Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour*, *46*(5), 999–1010. https://doi.org/10.1006/anbe.1993.1281

Heyes, Cecilia M., & Galef. (1996). *Social Learning In Animals: The Roots of Culture*. Elsevier.

Hisey, E., Kearney, M. G., & Mooney, R. (2018). A common neural circuit mechanism for internally guided and externally reinforced forms of motor learning. *Nature Neuroscience*, *21*(4), 589–597. https://doi.org/10.1038/s41593-018-0092-6

Holveck, M. J., & Riebel, K. (2007). Preferred songs predict preferred males: Consistency and repeatability of zebra finch females across three test contexts. *Animal Behaviour*, *74*(2), 297–309.

Holzhaider, J. C., Hunt, G. R., & Gray, R. D. (2010a). Social learning in new Caledonian crows. *Learning & Behavior*, *38*(3), 206–219. https://doi.org/10.3758/LB.38.3.206

Holzhaider, J. C., Hunt, G. R., & Gray, R. D. (2010b). The development of pandanus tool manufacture in wild New Caledonian crows. *Behaviour*, *147*(5/6), 553–586.

Horner, V., Whiten, A., Flynn, E., & Waal, F. B. M. de. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences*, *103*(37), 13878–13883. https://doi.org/10.1073/pnas.0606015103

Houx, A. B., & ten Cate, C. (1999). Song learning from playback in zebra finches: Is there an effect of operant contingency? *Animal Behaviour*, *57*(4), 837–845. https://doi.org/10.1006/anbe.1998.1046

Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, *379*(6562), 249–251. https://doi.org/10.1038/379249a0

Hunt, G. R., & Gray, R. D. (2003). Diversification and cumulative evolution in New Caledonian crow

tool manufacture. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1517), 867–874. https://doi.org/10.1098/rspb.2002.2302

Hunt, G. R., & Gray, R. D. (2006). Tool manufacture by New Caledonian crows: Chipping away at human uniqueness. *Acta Zoologica Sinica*, *52*(Supp), 622–625.

Hyland Bruno, J., & Tchernichovski, O. (2017). Regularities in zebra finch song beyond the repeated motif. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2017.11.001

Ikebuchi, M., & Okanoya, K. (1999). Male Zebra Finches and Bengalese Finches Emit Directed Songs to the Video Images of Conspecific Females Projected onto a TFT Display. *Zoological Science*, *16*(1), 63–70. https://doi.org/10.2108/zsj.16.63

Immelmann, K. (1962). Beiträge zu einer vergleichenden Biologie australischer Prachtfinken (Spermestidae). Jahr- biicher Abteilung fiir Systematik Okologie und Geographie der Tiere, 90, l-196.

Immelmann, K. (1969). Song development in the zebra finch and other estrildid finches. *Bird Vocalizations*, *61*.

Ince, S. A., Slater, P. J. B., & Weismann, C. (1980). Changes with time in the songs of a population of chaffinches. *Condor*, 285–290.

Iyengar, S., & Bottjer, S. W. (2002). The Role of Auditory Experience in the Formation of Neural Circuits Underlying Vocal Learning in Zebra Finches. *Journal of Neuroscience*, *22*(3), 946–958. https://doi.org/10.1523/JNEUROSCI.22-03-00946.2002

Janik, V. M. (2014). Cetacean vocal learning and communication. *Current Opinion in Neurobiology*, *28*, 60–65. https://doi.org/10.1016/j.conb.2014.06.010

Janik, V. M., & Slater, P. J. (1997). Vocal learning in mammals. *Advances in the Study of Behaviour*, *26*, 59–100.

Janik, V. M., & Slater, P. J. (2003). Traditions in mammalian and avian vocal communication. *The Biology of Traditions: Models and Evidence*, 213–235.

Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, *60*(1), 1–11. https://doi.org/10.1006/anbe.2000.1410

Jarvis, E. D. (2019). Evolution of vocal learning and spoken language. *Science*, *366*(6461), 50–54.

https://doi.org/10.1126/science.aax0287

Jeannin, S., Gilbert, C., & Leboucher, G. (2017). Effect of interaction type on the characteristics of pet-directed speech in female dog owners. *Animal Cognition*, *20*(3), 499–509. https://doi.org/10.1007/s10071-017-1077-7

Jenkins, P. F. (1978). Cultural transmission of song patterns and dialect development in a free-living bird population. *Animal Behaviour*, *26*, 50–78. https://doi.org/10.1016/0003-3472(78)90007-6

Jones, A. E., & Slater, P. J. B. (1996). The Role of Aggression in Song Tutor Choice in the Zebra Finch: Cause or Effect? *Behaviour*, *133*(1/2), 103–115.

Kaminski, J., Call, J., & Fischer, J. (2004). Word Learning in a Domestic Dog: Evidence for 'Fast Mapping'. *Science*, *304*(5677), 1682–1683. https://doi.org/10.1126/science.1097859

Kao, M. H., & Brainard, M. S. (2006). Lesions of an Avian Basal Ganglia Circuit Prevent Context-Dependent Changes to Song Variability. *Journal of Neurophysiology*, *96*(3), 1441–1455. https://doi.org/10.1152/jn.01138.2005

Katz, M., & Lachlan, R. F. (2003). Social learning of food types in zebra finches (*Taenopygia guttata*) is directed by demonstrator sex and feeding activity. *Animal Cognition*, *6*(1), 11–16. https://doi.org/10.1007/s10071-003-0158-y

Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. *Primates*, *6*(1), 1–30. https://doi.org/10.1007/BF01794457

Kawamura, S. (1954). On a new type of feeding habit which developed in a group of wild Japanese monkeys. *Seibutsu-Shinka*, *2*, 11–13.

Kenward, B., Rutz, C., Weir, A. A., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behaviour*, *72*(6), 1329–1343.

Kenward, B., Weir, A. A. S., Rutz, C., & Kacelnik, A. (2005). Tool manufacture by naive juvenile crows. *Nature*, *433*(7022), 121–121. https://doi.org/10.1038/433121a

King, A. P., & West, M. J. (1983). Epigenesis of cowbird song—A joint endeavour of males and females. *Nature*, *305*(5936), 704–706. https://doi.org/10.1038/305704a0

King, A. P., West, M. J., & Eastzer, D. H. (1980). Song structure and song development as potential contributors to reproductive isolation in cowbirds (*Molothrus ater*). *Journal of Comparative*

and Physiological Psychology, *94*(6), 1028–1039. https://doi.org/10.1037/h0077737

Kirby, S., Cornish, H., & Smith, K. (2008). Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. *Proceedings of the National Academy of Sciences*, *105*(31), 10681–10686.

Kirby, S., Griffiths, T., & Smith, K. (2014). Iterated learning and the evolution of language. *Current Opinion in Neurobiology*, *28*, 108–114. https://doi.org/10.1016/j.conb.2014.07.014

Konishi, M. (1965). The Role of Auditory Feedback in the Control of Vocalization in the White-Crowned Sparrow. *Zeitschrift Für Tierpsychologie*, *22*(7), 770–783. https://doi.org/10.1111/j.1439-0310.1965.tb01688.x

Kopps, A. M., Ackermann, C. Y., Sherwin, W. B., Allen, S. J., Bejder, L., & Krützen, M. (2014). Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1782), 20133245. https://doi.org/10.1098/rspb.2013.3245

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

Krebs, J. R., & Kroodsma, D. E. (1980). Repertoires and Geographical Variation in Bird Song. In J. S. Rosenblatt, R. A. Hinde, C. Beer, & M.-C. Busnel (Eds.), *Advances in the Study of Behavior* (Vol. 11, pp. 143–177). https://doi.org/10.1016/S0065-3454(08)60117-5

Kroodsma, D. E. (2004). The diversity and plasticity of birdsong. Nature's music: the science of birdsong, 108-131.

Krützen, M., Kreicker, S., MacLeod, C. D., Learmonth, J., Kopps, A. M., Walsham, P., & Allen, S. J. (2014). Cultural transmission of tool use by Indo-Pacific bottlenose dolphins (*Tursiops sp.)* provides access to a novel foraging niche. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1784), 20140374. https://doi.org/10.1098/rspb.2014.0374

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences*, *102*(25), 8939–8943. https://doi.org/10.1073/pnas.0500232102

Kummer, H. (1971). *Primate Societies. Chicago and New York*. Aldine and Atherton.

Lachlan, R. F., Ratmann, O., & Nowicki, S. (2018). Cultural conformity generates extremely stable

traditions in bird song. *Nature Communications*, *9*(1), 2417. https://doi.org/10.1038/s41467-018-04728-1

Lachlan, R. F., & Servedio, M. R. (2004). Song Learning Accelerates Allopatric Speciation. *Evolution*, *58*(9), 2049–2063. https://doi.org/10.1111/j.0014-3820.2004.tb00489.x

Lachlan, R. F., & Slater, P. J. B. (2003). Song learning by chaffinches: How accurate, and from where? *Animal Behaviour*, *65*(5), 957–969. https://doi.org/10.1006/anbe.2003.2091

Lachlan, R. F., van Heijningen, C. A., ter Haar, S. M., & ten Cate, C. (2016). Zebra Finch Song Phonology and Syntactical Structure across Populations and Continents—A Computational Comparison. *Frontiers in Psychology*, *7*. Retrieved from http://www.ncbi.nlm.nih.gov/pmc/articles/PMC4935685/

Lachlan, R. F., Verzijden, M. N., Bernard, C. S., Jonker, P.-P., Koese, B., Jaarsma, S., Spoor, W., Slater, P. J. B, & ten Cate, C. (2013). The progressive loss of syntactical structure in bird song along an island colonization chain. *Current Biology*, *23*(19), 1896–1901.

Laiolo, P., & Tella, J. L. (2007). Erosion of animal cultures in fragmented landscapes. *Frontiers in Ecology and the Environment*, *5*(2), 68–72.

Laland, K. N. (2008). Animal cultures. *Current Biology*, *18*(9), R366–R370.

Laland, K. N., & Galef, B. G. (2009). *The question of animal culture*. Harvard University Press.

Laland, K. N., & Hoppitt, W. (2003). Do animals have culture? *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(3), 150–159. https://doi.org/10.1002/evan.10111

Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, *21*(10), 542–547.

Laland, K. N., Kendal, J. R., & Kendal, R. L. (2009). Animal culture: Problems and solutions. *The Question of Animal Culture*, 174–197.

Laland, K. N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, *9*(5), 493–499. https://doi.org/10.1093/beheco/9.5.493

Lauay, C., Gerlach, N. M., Adkins-Regan, E., & DeVoogd, T. J. (2004). Female zebra finches require early song exposure to prefer high-quality song as adults. *Animal Behaviour*, *68*(6), 1249–1255. https://doi.org/10.1016/j.anbehav.2003.12.025

Leboucher, G., Vallet, E., Nagle, L., Béguin, N., Bovet, D., Hallé, F., Draganoiu, T. I., Amy, M., & Kreutzer, M. (2012). Studying female reproductive activities in relation to male song: The domestic canary as a model. In *Advances in the Study of Behavior* (Vol. 44, pp. 183–223). Elsevier.

Lefebvre, L. (1995). The opening of milk bottles by birds: Evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission. *Behavioural Processes*, *34*(1), 43–53. https://doi.org/10.1016/0376-6357(94)00051-H

Lindauer, M. (1985). The dance language of honeybees: The history of a discovery.

Lipkind, D., Marcus, G. F., Bemis, D. K., Sasahara, K., Jacoby, N., Takahasi, M., Suzuki, K., Féher, O., Ravbar, P., Okanoya, K., & Tchernichovski, O. (2013). Stepwise acquisition of vocal combinatorial capacity in songbirds and human infants. *Nature*, *498*(7452), 104–108. https://doi.org/10.1038/nature12173

Lipkind, D., & Tchernichovski, O. (2011). Quantification of developmental birdsong learning from the subsyllabic scale to cultural evolution. *Proceedings of the National Academy of Sciences*, *108*(Supplement 3), 15572–15579. https://doi.org/10.1073/pnas.1012941108

Lipkind, D., Zai, A. T., Hanuschkin, A., Marcus, G. F., Tchernichovski, O., & Hahnloser, R. H. R. (2017). Songbirds work around computational complexity by learning song vocabulary independently of sequence. *Nature Communications*, *8*(1), 1–11. https://doi.org/10.1038/s41467-017-01436-0

Liu, H. M., Kuhl, P. K., & Tsao, F.-M. (2003). An association between mothers' speech clarity and infants' speech discrimination skills. *Developmental Science*, *6*(3), F1–F10. https://doi.org/10.1111/1467-7687.00275

Liu, W., Gardner, T. J., & Nottebohm, F. (2004). Juvenile zebra finches can use multiple strategies to learn the same song. *Proceedings of the National Academy of Sciences*, *101*(52), 18177–18182. https://doi.org/10.1073/pnas.0408065101

Liu, W., Kohn, J., Szwed, S. K., Pariser, E., Sepe, S., Haripal, B., Oshimori, N., Marsala, M., Miyanohara, A., & Lee, R. (2015). Human mutant huntingtin disrupts vocal learning in transgenic songbirds. *Nature Neuroscience*, *18*(11), 1617–1622.

https://doi.org/10.1038/nn.4133

Ljubičić, I., Hyland Bruno, J., & Tchernichovski, O. (2016). Social influences on song learning. *Current Opinion in Behavioral Sciences*, *7*, 101–107. https://doi.org/10.1016/j.cobeha.2015.12.006

Logan, C. J., Breen, A. J., Taylor, A. H., Gray, R. D., & Hoppitt, W. J. E. (2016). How New Caledonian crows solve novel foraging problems and what it means for cumulative culture. *Learning & Behavior*, *44*(1), 18–28. https://doi.org/10.3758/s13420-015-0194-x

Luther, D., & Baptista, L. (2010). Urban noise and the cultural evolution of bird songs. *Proceedings of the Royal Society of London B: Biological Sciences*, *277*(1680), 469–473.

MacDougall-Shackleton, E. A., & MacDougall-Shackleton, S. A. (2001). Cultural and Genetic Evolution in Mountain White-Crowned Sparrows: Song Dialects Are Associated with Population Structure. *Evolution*, *55*(12), 2568–2575. https://doi.org/10.1111/j.0014-3820.2001.tb00769.x

MacDougall-Shackleton, S. A., MacDougall-Shackleton, E. A., & Hahn, T. P. (2001). Physiological and behavioural responses of female mountain white-crowned sparrows to natal-and foreign-dialect songs. *Canadian Journal of Zoology*, *79*(2), 325–333.

Madden, J. R. (2008). Do bowerbirds exhibit cultures? *Animal Cognition*, *11*(1), 1–12. https://doi.org/10.1007/s10071-007-0092-5

Madden, J. R., Lowe, T. J., Fuller, H. V., Dasmahapatra, K. K., & Coe, R. L. (2004). Local traditions of bower decoration by spotted bowerbirds in a single population. *Animal Behaviour*, *68*(4), 759–765. https://doi.org/10.1016/j.anbehav.2003.12.007

Mainwaring, M. C., Beal, J. L., & Hartley, I. R. (2011). Zebra finches are bolder in an asocial, rather than social, context. *Behavioural Processes*, *87*(2), 171–175. https://doi.org/10.1016/j.beproc.2011.03.005

Mammen, D. L., & Nowicki, S. (1981). Individual differences and within-flock convergence in chickadee calls. *Behavioral Ecology and Sociobiology*, *9*(3), 179–186. https://doi.org/10.1007/BF00302935

Mariette, M. M., & Griffith, S. C. (2012). Nest visit synchrony is high and correlates with reproductive success in the wild Zebra finch *Taeniopygia guttata*. *Journal of Avian Biology*, *43*(2), 131–140.

https://doi.org/10.1111/j.1600-048X.2012.05555.x

Marler, P., & Tamura, M. (1962). Song 'Dialects' in Three Populations of White-Crowned Sparrows. *The Condor*, *64*(5), 368–377. https://doi.org/10.2307/1365545

Marler, P., & Tamura, M. (1964). Culturally transmitted patterns of vocal behavior in sparrows. *Science*, *146*(3650), 1483–1486.

Marler, P. (1970). A comparative approach to vocal learning: Song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology*, *71*(2, Pt.2), 1–25. https://doi.org/10.1037/h0029144

Martins, T. L. F., Roberts, M. L., Giblin, I., Huxham, R., & Evans, M. R. (2007). Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. *Hormones and Behavior*, *52*(4), 445–453. https://doi.org/10.1016/j.yhbeh.2007.06.007

McGrew, W. C. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge University Press.

Mennill, D. J., Doucet, S. M., Newman, A. E. M., Williams, H., Moran, I. G., Thomas, I. P., Woodworth, B. K., & Norris, D. R. (2018). Wild Birds Learn Songs from Experimental Vocal Tutors. *Current Biology*, *28*(20), 3273-3278.e4. https://doi.org/10.1016/j.cub.2018.08.011

Menyhart, O., Kolodny, O., Goldstein, M. H., DeVoogd, T. J., & Edelman, S. (2015). Juvenile zebra finches learn the underlying structural regularities of their fathers' song. *Frontiers in Psychology*, *6*.

Mery, F., Varela, S. A. M., Danchin, É., Blanchet, S., Parejo, D., Coolen, I., & Wagner, R. H. (2009). Public Versus Personal Information for Mate Copying in an Invertebrate. *Current Biology*, *19*(9), 730–734. https://doi.org/10.1016/j.cub.2009.02.064

Mesoudi, A. (2016). Cultural Evolution: A Review of Theory, Findings and Controversies. *Evolutionary Biology*, *43*(4), 481–497. https://doi.org/10.1007/s11692-015-9320-0

Mesoudi, A. (2017). Pursuing Darwin's curious parallel: Prospects for a science of cultural evolution. *Proceedings of the National Academy of Sciences*, *114*(30), 7853–7860. https://doi.org/10.1073/pnas.1620741114

Mets, D. G., & Brainard, M. S. (2018). Genetic variation interacts with experience to determine

interindividual differences in learned song. *Proceedings of the National Academy of Sciences*, *115*(2), 421–426. https://doi.org/10.1073/pnas.1713031115

Miller, A. H. (1956). Ecologic Factors that Accelerate Formation of Races and Species of Terrestrial Vertebrates. *Evolution*, *10*(3), 262–277. https://doi.org/10.2307/2406011

Miller, D. B. (1979a). Long-term recognition of father's song by female zebra finches. *Nature*, *280*, 389–391.

Miller, D. B. (1979b). The acoustic basis of mate recognition by female zebra finches (*Taeniopygia guttata*). *Animal Behaviour*, *27*, 376–380.

Morgan, T. J. H., & Laland, K. N. (2012). The Biological Bases of Conformity. *Frontiers in Neuroscience*, *6*. https://doi.org/10.3389/fnins.2012.00087

Morton, E. S. (1975). Ecological Sources of Selection on Avian Sounds. *The American Naturalist*, *109*(965), 17–34. https://doi.org/10.1086/282971

Moseley, D. L., Phillips, J. N., Derryberry, E. P., & Luther, D. A. (2019). Evidence for differing trajectories of songs in urban and rural populations. *Behavioral Ecology*. https://doi.org/10.1093/beheco/arz142

Mundinger, P. C. (1970). Vocal Imitation and Individual Recognition of Finch Calls. *Science*, *168*(3930), 480–482. https://doi.org/10.1126/science.168.3930.480

Mundinger, P. C. (1980). Animal cultures and a general theory of cultural evolution. *Ethology and Sociobiology*, *1*(3), 183–223. https://doi.org/10.1016/0162-3095(80)90008-4

Nagle, L., & Kreutzer, M. L. (1997). Adult female domesticated canaries can modify their song preferences. *Canadian Journal of Zoology*, *75*(8), 1346–1350. https://doi.org/10.1139/z97-759

Naguib, M., Flörcke, C., & Oers, K. van. (2011). Effects of social conditions during early development on stress response and personality traits in great tits (*Parus major*). *Developmental Psychobiology*, *53*(6), 592–600. https://doi.org/10.1002/dev.20533

Nettle, D. (1999). Linguistic Diversity. New York: Oxford University Press.

Niyogi, P. (2006). *The computational nature of language learning and evolution*. MIT press Cambridge, MA.

Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M. N., & Jenner, K. C. S. (2000). Cultural revolution

in whale songs. *Nature*, *408*(6812), 537–537. https://doi.org/10.1038/35046199

Nottebohm, F. (1969). The song of the chingolo, *Zonotrichia capensis*, in Argentina: Description and evaluation of a system of dialects. *The Condor*, *71*(3), 299–315.

Nottebohm, F. (1972). The Origins of Vocal Learning. *The American Naturalist*, *106*(947), 116–140. https://doi.org/10.1086/282756

Nottebohm, F., Stokes, T. M., & Leonard, C. M. (1976). Central control of song in the canary, *Serinus canarius*. *Journal of Comparative Neurology*, *165*(4), 457–486.

Nowak, M. A., Komarova, N. L., & Niyogi, P. (2002). Computational and evolutionary aspects of language. *Nature*, *417*(6889), 611–617. https://doi.org/10.1038/nature00771

Nowicki, S., Hasselquist, D., Bensch, S., & Peters, S. (2000). Nestling growth and song repertoire size in great reed warblers: Evidence for song learning as an indicator mechanism in mate choice. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1460), 2419–2424. https://doi.org/10.1098/rspb.2000.1300

Nowicki, S., & Searcy, W. A. (2011). Are better singers smarter? *Behavioral Ecology*, *22*(1), 10–11.

Odom, K. J., Hall, M. L., Riebel, K., Omland, K. E., & Langmore, N. E. (2014). Female song is widespread and ancestral in songbirds. *Nature Communications*, *5*(1), 1–6. https://doi.org/10.1038/ncomms4379

Okanoya, K. (2004). The Bengalese Finch. *Ann. NY Acad. Sci*, *1016*, 724–735.

O'Loghlen, A. L., Ellis, V., Zaratzian, D. R., Merrill, L., & Rothstein, S. I. (2011). Cultural Evolution and Long-Term Song Stability in a Dialect Population of Brown-Headed Cowbirds. *The Condor*, *113*(2), 449–461. https://doi.org/10.1525/cond.2011.100103

O'Loghlen, A. L., Merrill, L., & Rothstein, S. I. (2013). Fidelity of Song Imitation and Stability of Dialect Songs in Brown-Headed Cowbirds. *The Condor*, *115*(3), 677–686. https://doi.org/10.1525/cond.2013.120073

O'Loghlen, A. L., & Rothstein, S. I. (1995). Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. *Behavioral Ecology and Sociobiology*, *36*(4), 251–259. https://doi.org/10.1007/BF00165834

O'Loghlen, A. L., & Rothstein, S. I. (2003). Female preference for the songs of older males and the

maintenance of dialects in brown-headed cowbirds (*Molothrus ater*). *Behavioral Ecology and Sociobiology*, *53*(2), 102–109. https://doi.org/10.1007/s00265-002-0551-6

Parker, K. A., Anderson, M. J., Jenkins, P. F., & Brunton, D. H. (2012). The effects of translocation-induced isolation and fragmentation on the cultural evolution of bird song. *Ecology Letters*, *15*(8), 778–785.

Patricelli, G. L., Coleman, S. W., & Borgia, G. (2006). Male satin bowerbirds, *Ptilonorhynchus violaceus*, adjust their display intensity in response to female startling: An experiment with robotic females. *Animal Behaviour*, *71*(1), 49–59. https://doi.org/10.1016/j.anbehav.2005.03.029

Patricelli, G. L., & Krakauer, A. H. (2010). Tactical allocation of effort among multiple signals in sage grouse: An experiment with a robotic female. *Behavioral Ecology*, *21*(1), 97–106. https://doi.org/10.1093/beheco/arp155

Payne, K., & Payne, R. (1985). Large Scale Changes over 19 Years in Songs of Humpback Whales in Bermuda. *Zeitschrift Für Tierpsychologie*, *68*(2), 89–114. https://doi.org/10.1111/j.1439-0310.1985.tb00118.x

Payne, R. B. (1981). *Population structure and social behaviour: Models for testing the ecological significance of song dialects in birds. In: Alexander RD & Tinkle DW (eds): Natural selection and social behaviour: Recent Research and New Theory*. Chiron Press. New York: 108.

Payne, R. B. (1982). Ecological Consequences of Song Matching: Breeding Success and Intraspecific Song Mimicry in Indigo Buntings. *Ecology*, *63*(2), 401–411. https://doi.org/10.2307/1938958

Payne, R. B. (1983). The social context of song mimicry: Song-matching dialects in indigo buntings (*Passerina cyanea*). *Animal Behaviour*, *31*(3), 788–805. https://doi.org/10.1016/S0003-3472(83)80236-X

Payne, R. B., Thompson, W. L., Fiala, K. L., & Sweany, L. L. (1981). Local Song Traditions in Indigo Buntings: Cultural Transmission of Behavior Patterns across Generations. *Behaviour*, *77*(4), 199–221.

Payne, R. B. (1996). Song traditions in indigo buntings: Origin, improvisation, dispersal, and extinction in cultural evolution. *Ecology and Evolution of Acoustic Communication in Birds*, 198–220.

Payne, R. B., & Payne, L. L. (1997). Field observations, experimental design, and the time and place of learning bird songs. https://doi.org/10.1017/CBO9780511758843.005

Perez, E. C., Elie, J. E., Soulage, C. O., Soula, H. A., Mathevon, N., & Vignal, C. (2012). The acoustic expression of stress in a songbird: Does corticosterone drive isolation-induced modifications of zebra finch calls? *Hormones and Behavior*, *61*(4), 573–581. https://doi.org/10.1016/j.yhbeh.2012.02.004

Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., … Rose, L. (2003). Social Conventions in Wild White-faced Capuchin Monkeys: Evidence for Traditions in a Neotropical Primate. *Current Anthropology*, *44*(2), 241–268. https://doi.org/10.1086/345825

Peters, S., Searcy, W. A., & Nowicki, S. (2014). Developmental stress, song-learning, and cognition. *Integrative and Comparative Biology*, *54*(4), 555–567.

Petkov, C. I., & Jarvis, E. (2012). Birds, primates, and spoken language origins: Behavioral phenotypes and neurobiological substrates. *Frontiers in Evolutionary Neuroscience*, *4*. https://doi.org/10.3389/fnevo.2012.00012

Pipek, P., Petrusková, T., Petrusek, A., Diblíková, L., Eaton, M. A., & Pyšek, P. (2018). Dialects of an invasive songbird are preserved in its invaded but not native source range. *Ecography*, *41*(2), 245–254. https://doi.org/10.1111/ecog.02779

Podos, J. (2001). Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature*, *409*(6817), 185–188. https://doi.org/10.1038/35051570

Podos, J. (2018). Animal Behavior: Song Learning out of the Box. *Current Biology*, *28*(20), R1195–R1197. https://doi.org/10.1016/j.cub.2018.08.054

Podos, J., & Nowicki, S. (2004). Beaks, adaptation, and vocal evolution in Darwin's finches. *AIBS Bulletin*, *54*(6), 501–510.

Podos, J., & Warren, P. S. (2007). The Evolution of Geographic Variation in Birdsong. In *Advances in the Study of Behavior* (Vol. 37, pp. 403–458). https://doi.org/10.1016/S0065-3454(07)37009-5

Price, P. H. (1979). Developmental determinants of structure in zebra finch song. *Journal of Comparative and Physiological Psychology*, *93*(2), 260–277. https://doi.org/10.1037/h0077553

Ravbar, P., Lipkind, D., Parra, L. C., & Tchernichovski, O. (2012). Vocal exploration is locally regulated

during song learning. *The Journal of Neuroscience*, *32*(10), 3422–3432.

Reichmuth, C., & Casey, C. (2014). Vocal learning in seals, sea lions, and walruses. *Current Opinion in Neurobiology*, *28*, 66–71. https://doi.org/10.1016/j.conb.2014.06.011

Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, *15*(2), 68–76. https://doi.org/10.1016/j.tics.2010.12.002

Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, *24*(2), 309–324. https://doi.org/10.1017/S0140525X0100396X

Riebel, K. (2000). Early exposure leads to repeatable preferences for male song in female zebra finches. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1461), 2553–2558.

Riebel, K. (2003). Developmental influences on auditory perception in female zebra finches—Is there a sensitive phase for song preference learning? *Animal Biology*, *53*(2), 73–87. https://doi.org/10.1163/157075603769700304

Riebel, K. (2009). Song and female mate choice in zebra finches: A review. *Advances in the Study of Behavior*, *40*, 197–238.

Riebel, K., Smallegange, I. M., Terpstra, N. J., & Bolhuis, J. J. (2002). Sexual equality in zebra finch song preference: Evidence for a dissociation between song recognition and production learning. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1492), 729–733. https://doi.org/10.1098/rspb.2001.1930

Riebel, K., Spierings, M. J., Holveck, M. J., & Verhulst, S. (2012). Phenotypic plasticity of avian social-learning strategies. *Animal Behaviour*, *84*(6), 1533–1539. https://doi.org/10.1016/j.anbehav.2012.09.029

Roberts, T. F., Tschida, K. A., Klein, M. E., & Mooney, R. (2010). Rapid spine stabilization and synaptic enhancement at the onset of behavioural learning. *Nature*, *463*(7283), 948–952. https://doi.org/10.1038/nature08759

Rosa, P., Nguyen, V., & Dubois, F. (2012). Individual differences in sampling behaviour predict social information use in zebra finches. *Behavioral Ecology and Sociobiology*, *66*(9), 1259–1265.

https://doi.org/10.1007/s00265-012-1379-3

Rothstein, S. I., & Fleischer, R. C. (1987). Vocal Dialects and Their Possible Relation to Honest Status Signalling in the Brown-Headed Cowbird. *The Condor*, *89*(1), 1–23. https://doi.org/10.2307/1368756

Rout, T. M., Hauser, C. E., & Possingham, H. P. (2007). Minimise long-term loss or maximise short-term gain?: Optimal translocation strategies for threatened species. *Ecological Modelling*, *201*(1), 67–74. https://doi.org/10.1016/j.ecolmodel.2006.07.022

Rutz, C., Bluff, L. A., Weir, A. A. S., & Kacelnik, A. (2007). Video Cameras on Wild Birds. *Science*, *318*(5851), 765–765. https://doi.org/10.1126/science.1146788

Ryan, M. J., & Brenowitz, E. A. (1985). The Role of Body Size, Phylogeny, and Ambient Noise in the Evolution of Bird Song. *The American Naturalist*, *126*(1), 87–100. https://doi.org/10.1086/284398

Sasaki, T., & Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications*, *8*(1), 1–6. https://doi.org/10.1038/ncomms15049

Scharff, C., & Nottebohm, F. (1991). A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: Implications for vocal learning. *Journal of Neuroscience*, *11*(9), 2896–2913. https://doi.org/10.1523/JNEUROSCI.11-09-02896.1991

Searcy, W. A., & Nowicki, S. (2019). Birdsong learning, avian cognition and the evolution of language. *Animal Behaviour*, *151*, 217–227. https://doi.org/10.1016/j.anbehav.2019.01.015

Searcy, W. A., & Andersson, M. (1986). Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, *17*(1), 507–533.

Searcy, W.A. & Yasukawa, K. (1996). Song and female choice. *In: Kroodsma, D.E., Miller, E.H. (Eds.), Ecology and Evolution of Acoustic Communication in Birds. Comstock Publishing Associates, Ithaca*, pp. 454–473.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, *210*(4471), 801–803. https://doi.org/10.1126/science.7433999

Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*,

34(6), 1640–1658. https://doi.org/10.1016/S0003-3472(86)80252-4

Shank, S. S., & Margoliash, D. (2009). Sleep and sensorimotor integration during early vocal learning in a songbird. *Nature*, *458*(7234), 73–77. https://doi.org/10.1038/nature07615

Slabbekoorn, H., & Peet, M. (2003). Ecology: Birds sing at a higher pitch in urban noise. *Nature*, *424*(6946), 267.

Slabbekoorn, H., & Ripmeester, E. a. P. (2008). Birdsong and anthropogenic noise: Implications and applications for conservation. *Molecular Ecology*, *17*(1), 72–83. https://doi.org/10.1111/j.1365-294X.2007.03487.x

Slabbekoorn, H., & Smith, T. B. (2002). Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*. Retrieved from https://royalsocietypublishing.org/doi/abs/10.1098/rstb.2001.1056

Slater, P. J. B. (1985). White rats and general theories. *Behavioral and Brain Sciences*, *8*(1), 115–116. https://doi.org/10.1017/S0140525X00019944

Slater, P. J. B. (1986). The cultural transmission of bird song. *Trends in Ecology & Evolution*, *1*(4), 94–97. https://doi.org/10.1016/0169-5347(86)90032-7

Slater, P. J. B., Eales, L. A., & Clayton, N. S. (1988). Song Learning in Zebra Finches (*Taeniopygia guttata*): Progress and Prospects. *Advances in the Study of Behavior*, *18*, 1.

Slater, P. J. B., & Ince, S. A. (1979). Cultural Evolution in Chaffinch Song. *Behaviour*, *71*(1–2), 146–166. https://doi.org/10.1163/156853979X00142

Slater, P. J. B. (1989). Bird song learning: Causes and consequences. *Ethology Ecology & Evolution*, *1*(1), 19–46. https://doi.org/10.1080/08927014.1989.9525529

Slater, P. J. B., & Mann, N. I. (2004). Why do the females of many bird species sing in the tropics? *Journal of Avian Biology*, *35*(4), 289–294. https://doi.org/10.1111/j.0908-8857.2004.03392.x

Smith, T. G., Siniff, D. B., Reichle, R., & Stone, S. (1981). Coordinated behavior of killer whales, *Orcinus orca*, hunting a crabeater seal, *Lobodon carcinophagus*. *Canadian Journal of Zoology*, *59*(6), 1185–1189. https://doi.org/10.1139/z81-167

Snowdon, C. T. (2009). Plasticity of Communication in Nonhuman Primates. In *Advances in the Study of Behavior*, *40*, 239-276.

Soha, J. A., Nelson, D. A., & Parker, P. G. (2004). Genetic analysis of song dialect populations in Puget Sound white-crowned sparrows. *Behavioral Ecology*, *15*(4), 636–646. https://doi.org/10.1093/beheco/arh055

Sossinka, R., & Böhner, J. (1980). Song types in the zebra finch *Poephila guttata castanotis*. *Zeitschrift Für Tierpsychologie*, *53*(2), 123–132.

Spierings, M. J., & ten Cate, C. (2016). Budgerigars and zebra finches differ in how they generalize in an artificial grammar learning experiment. *Proceedings of the National Academy of Sciences*, *113*(27), E3977–E3984. https://doi.org/10.1073/pnas.1600483113

Stoddard, P. K., Beecher, M. D., Campbell, S. E., & Horning, C. L. (1992). Song-type matching in the song sparrow. *Canadian Journal of Zoology*, *70*(7), 1440–1444. https://doi.org/10.1139/z92-200

Stoeger, A. S., & Manger, P. (2014). Vocal learning in elephants: Neural bases and adaptive context. *Current Opinion in Neurobiology*, *28*, 101–107. https://doi.org/10.1016/j.conb.2014.07.001

St-Pierre, A., Larose, K., & Dubois, F. (2009). Long-term social bonds promote cooperation in the iterated Prisoner's Dilemma. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1676), 4223–4228. https://doi.org/10.1098/rspb.2009.1156

Sturdy, C. B., Phillmore, L. S., Sartor, J. J., & Weisman, R. G. (2001). Reduced social contact causes auditory perceptual deficits in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, *62*(6), 1207–1218. https://doi.org/10.1006/anbe.2001.1864

Suzuki, T. N., Griesser, M., & Wheatcroft, D. (2019). Syntactic rules in avian vocal sequences as a window into the evolution of compositionality. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2019.01.009

Svec, L. A., & Wade, J. (2009). Estradiol induces region-specific inhibition of ZENK but does not affect the behavioral preference for tutored song in adult female zebra finches. *Behavioural Brain Research*, *199*(2), 298–306. https://doi.org/10.1016/j.bbr.2008.12.006

Swaddle, J. P., McBride, L., & Malhotra, S. (2006). Female zebra finches prefer unfamiliar males but not when watching noninteractive video. *Animal Behaviour*, *72*(1), 161–167. https://doi.org/10.1016/j.anbehav.2005.12.005

Tchernichovski, O., Feher, O., Fimiarz, D., & Conley, D. (2017). How social learning adds up to a culture: From birdsong to human public opinion. *Journal of Experimental Biology*, *220*(1), 124–132. https://doi.org/10.1242/jeb.142786

Tchernichovski, O., & Lipkind, D. (2016). Encoding vocal culture. *Science*, *354*(6317), 1234–1235. https://doi.org/10.1126/science.aal3205

Tchernichovski, O., & Nottebohm, F. (1998). Social inhibition of song imitation among sibling male zebra finches. *Proceedings of the National Academy of Sciences*, *95*(15), 8951–8956.

Tchernichovski, O., Nottebohm, F., Ho, C. E., Pesaran, B., & Mitra, P. P. (2000). A procedure for an automated measurement of song similarity. *Animal Behaviour*, *59*(6), 1167–1176. https://doi.org/10.1006/anbe.1999.1416

Temeles, E. J. (1994). The role of neighbours in territorial systems: When are they 'dear enemies'? *Animal Behaviour*, *47*(2), 339–350. https://doi.org/10.1006/anbe.1994.1047

Templeton, C. N., Laland, K. N., & Boogert, N. J. (2014). Does song complexity correlate with problem-solving performance in flocks of zebra finches? *Animal Behaviour*, *92*, 63–71. https://doi.org/10.1016/j.anbehav.2014.03.019

ten Cate, C. (1991). Behaviour-contingent exposure to taped song and zebra finch song learning. *Animal Behaviour*, *42*(5), 857–859. https://doi.org/10.1016/S0003-3472(05)80131-9

ten Cate, C. (2014). On the phonetic and syntactic processing abilities of birds: From songs to speech and artificial grammars. *Current Opinion in Neurobiology*, *28*, 157–164. https://doi.org/10.1016/j.conb.2014.07.019

ten Cate, C. (2018). The comparative study of grammar learning mechanisms: Birds as models. *Current Opinion in Behavioral Sciences*, *21*, 13–18. https://doi.org/10.1016/j.cobeha.2017.11.008

Ter Maat, A., Trost, L., Sagunsky, H., Seltmann, S., & Gahr, M. (2014). Zebra finch mates use their forebrain song system in unlearned call communication. *PloS One*, *9*(10), e109334.

Thorpe, W. H. (1954). The process of song-learning in the chaffinch as studied by means of the sound spectrograph. *Nature*, *173*(4402), 465–469.

Todt, D., & Geberzahn, N. (2003). Age-dependent effects of song exposure: Song crystallization sets a boundary between fast and delayed vocal imitation. *Animal Behaviour*, *65*(5), 971–979.

https://doi.org/10.1006/anbe.2003.2127

Todt, D., & Naguib, M. (2000). Vocal Interactions in Birds: The Use of Song as a Model in Communication. In Peter J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, & T. J. Roper (Eds.), *Advances in the Study of Behavior* (Vol. 29, pp. 247–296). https://doi.org/10.1016/S0065-3454(08)60107-2

Tomasello, M. (1994). The question of chimpanzee culture. In *Chimpanzee cultures* (pp. 301–317). Cambridge, MA, US: Harvard University Press.

Tomback, D. F., & Baker, M. C. (1984). Assortative mating by white-crowned sparrows at song dialect boundaries. *Animal Behaviour*, *32*(2), 465–469. https://doi.org/10.1016/S0003-3472(84)80282-1

Trainer, J. M. (1983). Changes in Song Dialect Distributions and Microgeographic Variation in Song of White-Crowned Sparrows (*Zonotrichia leucophrys nuttalli*). *The Auk*, *100*(3), 568–582. https://doi.org/10.1093/auk/100.3.568

Trainer, J. M. (1989). Cultural evolution in song dialects of yellow-rumped caciques in Panama. *Ethology*, *80*(1–4), 190–204.

Trudgill, P. (1983). *On dialect: Social and geographical perspectives*. Wiley-Blackwell.

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent Social Learning and Conformity Shape a Wild Primate's Foraging Decisions. *Science*, *340*(6131), 483–485. https://doi.org/10.1126/science.1232769

van Heijningen, C. A. A., Chen, J., van Laatum, I., van der Hulst, B., & ten Cate, C. (2013). Rule learning by zebra finches in an artificial grammar learning task: Which rule? *Animal Cognition*, *16*(2), 165–175. https://doi.org/10.1007/s10071-012-0559-x

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S., & Merrill, M. (2003). Orangutan Cultures and the Evolution of Material Culture. *Science*, *299*(5603), 102–105. https://doi.org/10.1126/science.1078004

van Schaik, C. P., & Knott, C. D. (2001). Geographic variation in tool use on Neesia fruits in orangutans. *American Journal of Physical Anthropology*, *114*(4), 331–342. https://doi.org/10.1002/ajpa.1045

Vignal, C., Mathevon, N., & Mottin, S. (2004). Audience drives male songbird response to partner's voice. *Nature*, *430*(6998), 448–451.

Vignal, C., Mathevon, N., & Mottin, S. (2008). Mate recognition by female zebra finch: Analysis of individuality in male call and first investigations on female decoding process. *Behavioural Processes*, *77*(2), 191–198. https://doi.org/10.1016/j.beproc.2007.09.003

Wallschläger, D. (1980). Correlation of song frequency and body weight in passerine birds. *Experientia*, *36*(4), 412–412. https://doi.org/10.1007/BF01975119

Warner, R. R. (1988). Traditionality of mating-site preferences in a coral reef fish. *Nature*, *335*(6192), 719–721. https://doi.org/10.1038/335719a0

Warner, R. R. (1990). Male versus female influences on mating-site determination in a coral reef fish. *Animal Behaviour*, *39*(3), 540–548. https://doi.org/10.1016/S0003-3472(05)80420-8

Webb, B. (2008). Using Robots to Understand Animal Behavior. In *Advances in the Study of Behavior* (Vol. 38, pp. 1–58). https://doi.org/10.1016/S0065-3454(08)00001-6

Weilgart, L., & Whitehead, H. (1997). Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology*, *40*(5), 277–285. https://doi.org/10.1007/s002650050343

West, M. J., & King, A. P. (1988). Female visual displays affect the development of male song in the cowbird. *Nature*, *334*(6179), 244–246. https://doi.org/10.1038/334244a0

Wheelwright, N. T., Swett, M. B., Levin, I. I., Kroodsma, D. E., Freeman-Gallant, C. R., & Williams, H. (2008). The influence of different tutor types on song learning in a natural bird population. *Animal Behaviour*, *75*(4), 1479–1493. https://doi.org/10.1016/j.anbehav.2007.08.030

White, D. J., & Galef, B. G. (2000). Culture'in quail: Social influences on mate choices of female Coturnix japonica. *Animal Behaviour-London-Bailliere Tindall*, *59*(5), 975–979.

Whitehead, H., & Rendell, L. (2014). *The cultural lives of whales and dolphins*. University of Chicago Press.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*(6737), 682–685. https://doi.org/10.1038/21415

Whiten, A. (2000). Primate Culture and Social Learning. *Cognitive Science*, *24*(3), 477–508. https://doi.org/10.1207/s15516709cog2403_6

Whiten, A., Hinde, R. A., Laland, K. N., & Stringer, C. B. (2011). Culture evolves. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 938–948. https://doi.org/10.1098/rstb.2010.0372

Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, *437*(7059), 737–740. https://doi.org/10.1038/nature04047

Whiten, A., & Mesoudi, A. (2008). Establishing an experimental science of culture: Animal social diffusion experiments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1509), 3477–3488. https://doi.org/10.1098/rstb.2008.0134

Whitney, C. L. (1992). Temporal stability of song in a local population of Wood Thrushes. *The Wilson Bulletin*, *104*(3), 516–520.

Wiens, J. A. (1982). Song Pattern Variation in the Sage Sparrow (*Amphispiza belli*): Dialects or Epiphenomena? *The Auk*, *99*(2), 208–229. https://doi.org/10.1093/auk/99.2.208

Wiley, R. H. (1971). Song Groups in a Singing Assembly of Little Hermits. *The Condor*, *73*(1), 28–35. https://doi.org/10.2307/1366121

Williams, H. (1990). Models for song learning in the zebra finch: Fathers or others? *Animal Behaviour*, *39*(4), 745–757. https://doi.org/10.1016/S0003-3472(05)80386-0

Williams, H., Kilander, K., & Sotanski, M. L. (1993). Untutored song, reproductive success and song learning. *Animal Behaviour*, *45*(4), 695–705. https://doi.org/10.1006/anbe.1993.1084

Williams, H., Levin, I. I., Norris, D. R., Newman, A. E., & Wheelwright, N. T. (2013). Three decades of cultural evolution in Savannah sparrow songs. *Animal Behaviour*, *85*(1), 213–223.

Williams, H., & Staples, K. (1992). Syllable chunking in zebra finch (*Taeniopygia guttata*) song. *Journal of Comparative Psychology*, *106*(3), 278.

Wilson, E. O. (1975). Sociobiology: The New Synthesis. Cambridge, Massachusetts: Belknap Press.

Wood, W. E., & Yezerinac, S. M. (2006). Song Sparrow (*Melospiza Melodia*) Song Varies with Urban Noise. *The Auk*, *123*(3), 650–659. https://doi.org/10.1093/auk/123.3.650

Wright, T. F. (1996). Regional dialects in the contact call of a parrot. *Proceedings of the Royal Society*

of London. Series B: Biological Sciences, *263*(1372), 867–872. https://doi.org/10.1098/rspb.1996.0128

Wright, T. F., & Dahlin, C. R. (2018). Vocal dialects in parrots: Patterns and processes of cultural evolution. *Emu - Austral Ornithology*, *118*(1), 50–66. https://doi.org/10.1080/01584197.2017.1379356

Wright, T. F., Dahlin, C. R., & Salinas-Melgoza, A. (2008). Stability and change in vocal dialects of the yellow-naped amazon. *Animal Behaviour*, *76*(3), 1017–1027. https://doi.org/10.1016/j.anbehav.2008.03.025

Wright, T. F., & Wilkinson, G. S. (2001). Population genetic structure and vocal dialects in an amazon parrot. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1467), 609–616. https://doi.org/10.1098/rspb.2000.1403

Ydenberg, R. C., Giraldeau, L. A., & Falls, J. B. (1988). Neighbours, strangers, and the asymmetric war of attrition. *Animal Behaviour*, *36*(2), 343–347. https://doi.org/10.1016/S0003-3472(88)80004-6

Zajonc, R. B. (1965). Social Facilitation. *Science*, *149*(3681), 269–274.

Zann, R. A. (1990). Song and call learning in wild zebra finches in south-east Australia. *Animal Behaviour*, *40*(5), 811–828.

Zann, R. A. (1993). Variation in song structure within and among populations of Australian zebra finches. *The Auk*, 716–726.

Zann, R. A. (1996). *The zebra finch: A synthesis of field and laboratory studies* (Vol. 5). Oxford University Press.

Zevin, J. D., Seidenberg, M. S., & Bottjer, S. W. (2004). Limits on reacquisition of song in adult zebra finches exposed to white noise. *Journal of Neuroscience*, *24*(26), 5849–5862.

Appendices

Appendix I:

Substantial French Summary

Résumé de la thèse

Évolution culturelle du chant d'oiseau en laboratoire

Par Lucille Le Maguer

Sous la direction de Sébastien Derégnaucourt et Nicole Geberzahn

Cadre théorique

La culture animale

Bien que la culture ait, pendant longtemps, été considérée comme un phénomène définissant les civilisations humaines, depuis des années, un intérêt grandissant pour le sujet de la culture animale s'est développé et il existe désormais de nombreux exemples de cultures animales reconnus par la communauté scientifique. Une des définitions de la culture qui peut s'appliquer aussi bien aux êtres humains qu'aux animaux, est celle qui considère la culture comme un ensemble de savoirs et de pratiques socialement partagées et transmises qui se partagent et se transmettent socialement au sein d'un groupe donné et non par héritage génétique. Les exemples de cultures animales les plus célèbres sont sûrement : le comportement de lavage des pommes de terre chez les macaques japonais (*Macaca fuscata*); le large répertoire comportemental des chimpanzés (*Pan troglodytes*), incluant l'utilisation d'outils, le toilettage et les parades ; et enfin la pratique de perçage des opercules sur les bouteilles de lait chez les mésanges, en Grande Bretagne (*Parus major*, *Parus caeruleus* et *Periparus ater*).

Plus récemment, l'existence de traditions locales dans les méthodes de fourragements a été observée chez les mésanges charbonnières : des démonstrateurs capturés en nature étaient entraînés en laboratoire à ouvrir une mangeoire, en utilisant une seule technique sur les deux possibles. Les chercheurs ont observé que, une fois les démonstrateurs relâchés dans leur zone d'origine, la plupart des oiseaux confrontés à un démonstrateur utilisant la première technique reproduisaient cette même technique, sans chercher à utiliser l'autre. Ce pattern de transmission

culturelle a donc mené à des traditions locales stables sur deux générations, démontrant une grande conformité sociale entre les individus. La conformité culturelle étant un facteur clé dans l'évolution de la culture humaine, cette étude démontre que des comportement culturels complexes peuvent apparaître dans une large gamme taxonomique. En effet, des cultures animales ont été décrites aussi bien chez les mammifères tels que les primates (ex. chez les chimpanzés, les orangs-outans *Pongo pygmaeus* et les singes capucins *Cebus capucinus*) et les cétacés (ex. chez les baleines *Megaptera novaeangliae*, les orques *Orcinus orca* et les dauphins *Tursiops truncates*) ; que chez les oiseaux et les poissons. Outre chez les vertébrés, la culture a également été étudiée chez les insectes. De nos jours, avec les travaux approfondis sur les cultures chez divers taxons d'animaux et dans de multiples contextes comportementaux, il est difficile de douter de l'existence de cultures animales non humaines. Cependant, suite à ces découvertes, une nouvelle question s'est posée quant aux cultures animales : comment de telles cultures évoluent-elles dans le temps ?

L'évolution culturelle

L'évolution culturelle peut être définie comme l'altération ou le changement, d'une génération à l'autre, d'un trait de comportement appris. Pour qu'une culture émerge, trois stades sont nécessaires : 1) apparition d'une innovation (souvent de la part d'un seul individu) ; 2) transmission de cette innovation au travers d'un réseau social ; 3) modifications de cette innovation comportementale au niveau de la population. Selon la façon dont ces trois étapes se déroulent, les cultures en découlant peuvent évoluer différemment. Plusieurs auteurs ont suggéré que l'évolution culturelle puisse être évaluée à l'aide des mêmes concepts que ceux utilisés pour décrire l'évolution biologique. Les cultures animales seraient donc soumises à : 1) la variation (souvent due à des erreurs de copie), la sélection (en fonction de la fréquence à laquelle les individus utilisent ce trait comportemental) et l'héritabilité (permise par l'apprentissage social) ; 2) l'adaptation (c'est-à-dire si le comportement culturel procure un

avantage adaptatif ou non) ; 3) des variations géographiques ; 4) des accumulations de changements ou de modifications (un concept clé dans l'évolution des cultures humaines, qui se manifeste par une augmentation de la complexité et/ou de l'efficacité de la technologie au cours du temps).

Récemment, des auteurs ont suggéré que l'apprentissage social pouvait mener les cultures animales à évoluer de trois manières différentes. Dans ce cadre, les trois types de cultures animales dépendent de leur stabilité et de leur richesse: 1) dans une culture monolithique stable, une forte convergence culturelle mène à une grande conformité entre les individus (comme dans l'exemple précédemment évoqué chez les mésanges charbonnières) ; 2) dans une culture polymorphique stable, les individus montrent des combinaisons différentes de traits culturels et cependant ces traits restent stables au niveau de la population (c'est le cas notamment des cultures vocales chez les oiseaux dont nous parlerons plus tard) ; 3) dans une culture instable qui dérive, les traits culturels sont instables à la fois au niveau individuel et populationnel (c'est le cas, par exemple, des cultures vocales chez les baleines à bosse dont les mâles d'une même population se conforment à un type de chant, mais pas pour très longtemps). Pour finir, ces mêmes auteurs ont proposé un mécanisme d'équilibre entre des forces sociales convergentes et divergentes pouvant influencer l'évolution culturelle vers l'un ou l'autre de ces types de cultures. Par exemple, l'imitation serait une force convergente qui favoriserait la stabilité culturelle alors que les erreurs de copies constitueraient une force divergence qui l'affaiblirait. Cependant, nous ne savons pas encore bien comment la convergence due à l'imitation et la divergence due à l'accumulation d'erreurs de copies, se superposent pour expliquer l'émergence de cultures locales. Dans cette thèse, je démontrerai que de telles forces peuvent influer sur différentes parties du chant du diamant mandarin (*Taeniopygia guttata*), sans pour autant empêcher l’établissement de cultures vocales.

L'existence de cultures vocales ou dialectes chez les oiseaux

Chez de nombreuses communautés de vertébrés, la communication vocale permet de réguler les interactions sociales. Chez certaines espèces, ces interactions sont facilitées par l'apprentissage vocal, un processus par lequel un individu modifie la structure acoustique de ses vocalisations en imitant les productions vocales de ses congénères. Cette capacité est rare et on la trouve uniquement chez quelques mammifères (dont les humains) ainsi que chez trois groupes d'oiseaux dont les oiseaux chanteurs, aussi appelés oscines et appartenant à l'ordre des Passériformes. Cet apprentissage vocal est un prérequis évident à l'existence de cultures vocales et il a été démontré que des cultures vocales existaient chez les animaux non-humains et qu'elles constituaient un bon moyen d'aborder la question de l'évolution culturelle. En effet, dès l'Antiquité, on s'est intéressé au chant des oiseaux. Aristote avait notamment remarqué qu'il existait des variations géographiques au niveau du chant, qui renvoient aujourd'hui au terme de dialectes. Désormais, les dialectes vocaux (aussi appelés cultures vocales) et plus particulièrement les dialectes de chant chez les oiseaux chanteurs, constituent la forme de culture animale la plus largement étudiée et acceptée par la communauté scientifique. Ces dialectes de chant ont été décrits chez un grand nombre d'espèces d'oiseaux et il a été démontré que ces cultures vocales suivaient les forces évolutives mentionnées ci-dessus.

L'étude de cas la plus célèbre dans le domaine des dialectes de chant porte sur le bruant à couronne blanche (*Zonotrichia leucophrys nuttalli*), chez qui il a été démontré que les jeunes mâles apprenaient leur chant durant leur vie précoce, au travers de l'apprentissage social, en écoutant les mâles adultes environnants. Cette transmission culturelle du chant mène donc à de faibles variations du chant entre les individus d'une même population mais à de grandes différences dans la structure du chant des populations voisines. Dans ce contexte, les auteurs se réfèrent au terme de dialectes car la variation entre populations était plus importante que la variation au sein d'une même population. De manière générale, dans les dialectes de chant, les

traits culturels sont stables au niveau de la population car les individus d'une même aire géographique se conforment au même type de chant ; mais les individus montrent tout de même différentes combinaisons de ces traits qui mènent à des variations individuelles au niveau du chant, permettant ainsi la reconnaissance individuelle et la modulation d'interactions vocales entre oiseaux territoriaux. C'est pourquoi les dialectes de chant constituent un exemple parfait de culture polymorphique stable, comme mentionné précédemment. Cependant, les dialectes de chant peuvent tout de même varier au niveau de leur stabilité : dans certains cas, ils peuvent rester stables durant une longue période, parfois durant des décennies et possiblement durant des centaines de générations. Dans d'autres cas, les dialectes de chant peuvent rapidement apparaître et disparaître. Enfin, les dialectes de chant peuvent être distribués sur différentes échelles spatiales : du dialecte micro-géographique, entre très proches voisins, au dialecte macro-géographique s'étendant sur des milliers de kilomètres.

Les dialectes vocaux et leurs possibles fonctions restent un problème complexe à résoudre et trois hypothèses principales ont été énoncées : 1) l'hypothèse de l'adaptation génétique suggère que les dialectes servent d'outil nécessaire à l'appariement sexuel, les femelles préférant alors s'associer aux mâles chantant le dialecte local. Ainsi, ce phénomène inhiberait le flux génétique entre les différentes populations d'une même espèce et conduirait à des adaptations génétiques locales ; 2) l'hypothèse de l'adaptation sociale suggère que les dialectes constituent des marqueurs sociaux qui procureraient des avantages dans un contexte d'interactions sociales et/ou sexuelles : par exemple, des mâles partageant le même type de chant auraient moins d'interactions agressives entre eux et accèderaient plus facilement aux femelles. De plus, les dialectes sont également considérés comme des indicateurs d'appartenance au groupe et de résidence à long terme ; 3) enfin, l'hypothèse de l'épiphénomène suggère que les dialectes n'ont aucune fonction particulière et sont simplement un sous-produit de l'apprentissage vocal. Quoi qu'il en soit, les dialectes seraient particulièrement importants

chez les espèces sociales à forte mobilité, pour lesquelles les individus sont plus à même de rencontrer des congénères d'origines géographiques différentes. Au-delà de ces trois hypothèses, il a été démontré que les dialectes de chant ont joué un rôle important dans le processus de spéciation chez les Passériformes qui représentent le plus grand ordre d'oiseaux (avec le plus grand nombre d'espèces).

Pour finir, différents facteurs peuvent influencer l'évolution culturelle du chant, tels que 1) des influences sociales mais aussi génétiques sur les mécanismes de l'apprentissage vocal ; 2) la sélection sexuelle, les femelles démontrant des préférences pour certains types de chants comparés à d'autres mais pouvant aussi, potentiellement, influencer la stabilité des dialectes, en créant une pression de sélection sur les jeunes mâles, les poussant à se conformer au dialecte local; 3) les mécanismes de production sonore pouvant contraindre la capacité de l'oiseau à moduler son tractus vocal lors du chant, comme sa taille ou la morphologie de son bec; 4) des facteurs environnementaux et notamment anthropiques, comme le bruit urbain et la fragmentation des habitats.

Le chant d'oiseau comme modèle pour étudier l'évolution culturelle

Comprendre les origines et l'évolution des cultures humaines est délicat, notamment en raison du grand nombre d'années entre les générations mais aussi des problèmes éthiques liés à l'expérimentation. Bien que des paradigmes expérimentaux aient été utilisés chez l'être humain pour comprendre les mécanismes de l'évolution culturelle et notamment celle du langage, d'autres expérimentations, menées sur des animaux, ont démontré l'utilité du modèle animal et plus spécifiquement du modèle du chant d'oiseau, pour étudier ces aspects. En effet, de nombreux parallèles ont été mis en évidence entre la parole chez l'humain et le chant des oiseaux, tels que : l'importance des influences sociales sur le développement vocal ; l'importance du feedback auditif sur l'apprentissage et le maintien des vocalisations ; la latéralisation du cerveau concernant la production et la perception vocale. Bien que notre

connaissance de la culture vocale provienne des études de terrain, comprendre les rôles de l'apprentissage vocal dans le développement de la culture vocale nécessite des recherches en environnement contrôlé. Au cours d'une étude récente menée en laboratoire, des chercheurs ont étudié comment le chant évoluait au cours du temps au sein d'une colonie fondée à partir d'un individu élevé en isolement social pendant la période sensible d'apprentissage du chant. De la même façon que les enfants humains privés d'input linguistique au cours des premières années de la vie, les oiseaux chanteurs élevés en isolement social pendant les premiers mois suivant leur éclosion, développent des chants pauvres et anormaux qui diffèrent du type de chant spécifique observé en conditions naturelles. En utilisant le diamant mandarin, les auteurs ont observé que, dans des colonies fondées à partir d'individus isolés, le chant a évolué vers le type normal ("wild type") en trois à quatre générations. Cette expérience a confirmé le chant des oiseaux comme modèle biologique pour étudier l'évolution de la culture vocale en laboratoire.

Modèle biologique : le diamant mandarin

Le diamant mandarin domestique est une espèce originaire d'Australie. Elle est considérée comme hautement sociale car les diamant mandarins vivent en grandes colonies et forment des couples monogames maintenant des liens à vie. Ils se reproduisent rapidement et facilement en laboratoire et cette espèce est donc considérée comme la "souris volante" de la recherche sur le chant des oiseaux. En effet, avec son chant court et stéréotypé, le diamant mandarin a, depuis longtemps, été considéré comme un modèle de choix en neuro-éthologie.

Chez le diamant mandarin, seuls les mâles chantent et le chant est appris durant une phase sensible de la vie précoce (entre 25 et 90 jours suivant l'éclosion), en reproduisant le chant de mâles adultes (principalement celui du père). A l'issue de cette période sensible, le jeune mâle sera donc capable de produire un chant très similaire à celui du tuteur, et passés ces 90 jours, très peu de modifications du chant sont encore possibles. Le jeunes mâles sont capables d'apprentissage "vertical" (du père au fils) ou "oblique" (d'un adulte autre que le père

à un jeune), mais aussi d'apprentissage "horizontal" (entre jeunes du même âge). Chez cette espèce, le chant joue un rôle crucial dans le choix de partenaire sexuel et les femelles préfèrent les chants qu'elles ont entendus durant leur jeunesse. De ce fait, la préférence des femelles peut être un outil utile pour étudier la dynamique de l'évolution des chants d'oiseaux : les femelles préférant certains types de chants à d'autres, cela pourrait éventuellement conduire les chants des mâles à évoluer vers une certaine direction. Ceci est également corroboré par la récente découverte qui suggère que les femelles diamant mandarin pourraient guider le processus d'apprentissage vocal des mâles en donnant un feedback social en réponse à des vocalisations immatures.

Contrairement à ce qui a été observé chez de nombreuses espèces d'oiseaux chanteurs, il a été suggéré que les dialectes de chant ne peuvent pas apparaitre chez le diamant mandarin, ni dans la nature, ni en laboratoire. En effet, seules de très faibles variations au niveau du chant ont été décrites dans différentes zones géographiques d'Australie et il a été suggéré que la dispersion fréquente d'oiseaux entre les différentes populations empêcherait l'établissement de dialectes locaux. En laboratoire, une étude a proposé une hypothèse alternative : de nombreuses erreurs de copie lors de l'apprentissage du chant favoriseraient la variabilité intra-populationnelle et empêcheraient l'établissement de cultures vocales sur le long terme.

Objectif de la thèse

Cette thèse se propose d'utiliser des mesures comportementales en environnements sociaux contrôlés, afin de mieux comprendre les aspects dynamiques de l'évolution culturelle du chant chez l'oiseau. En utilisant le modèle de choix qu'est le diamant mandarin, trois expériences (correspondant aux trois chapitres de la thèse) ont été menées pour ce faire. Via une approche de laboratoire, cette thèse s'inscrit davantage dans un contexte théorique de mécanismes d'apprentissage du chant que dans une approche visant à reproduire ce qui pourrait se produire en conditions naturelles.

Chapitre 1 : Évolution culturelle du chant en laboratoire

En conditions naturelles, chaque diamant mandarin mâle produit un chant différent, constituant une signature individuelle. Cependant, dans ce 1er chapitre, je me suis intéressée à l'évolution du chant dans trois colonies de diamants mandarins particulières, dans lesquelles les mâles fondateurs produisaient tous un chant très similaire (une imitation du modèle de chant de la colonie). Cela a été réalisé en exposant plusieurs mâles à un modèle de chant unique (un motif de chant) durant leur phase sensible d'apprentissage. Une fois adultes, les mâles ayant le mieux reproduit le modèle de chant étaient choisis comme fondateurs pour les colonies. Dans deux colonies : colonie A1 et A2, les mâles fondateurs ont été exposés au modèle de chant A (Figure 1A) ; dans la troisième colonie, colonie B, les mâles fondateurs ont été exposés à un modèle de chant différent, le modèle B (Figure 1B). Dans de telles conditions artificielles, nous prédisions deux issues possibles: 1) soit les oiseaux d'une même colonie allaient innover et/ou faire des erreurs de copie lors de l'apprentissage du chant et donc diverger du modèle de chant originel de la colonie, ce qui entraînerait une forte diversité du chant au sein de chaque colonie et empêcherait l'établissement d'un dialecte spécifique à la colonie (comme suggéré précédemment par certains chercheurs) ; 2) soit les mâles allaient démontrer une grande conformité au modèle de chant, menant alors potentiellement à l'émergence d'un dialecte stable.

Pour suivre l'évolution du chant au fur et à mesure du temps dans les trois colonies, nous avons enregistré le chant de tous les mâles une fois adultes, en caisson d'isolation acoustique. Puis nous avons analysé toutes les unités de chant possibles chez ces oiseaux. En effet, le chant du diamant mandarin est organisé hiérarchiquement : le "motif" est défini comme une séquence courte et stéréotypée de sons appelés "syllabes", séparées les unes des autres par des intervalles de silence ; chaque syllabe étant elle-même composée de plusieurs petites unités appelées "éléments" et correspondant à des mouvements vocaux (Figure 1C). Enfin, l'unité la plus large du chant de diamant mandarin est appelée "phrase" ; chaque phrase est généralement constituée

de syllabes introductives, suivies d'un ou plusieurs motifs, parfois séparés par des syllabes d'une autre catégorie, appelées "connecteurs" (Figure 1C). Les connecteurs ressemblent, en général, à des cris produits lorsque l'oiseau perd ou cherche le contact avec des congénères. Enfin, puisque nous nous intéressions notamment à la comparaison entre le modèle de chant originel de chaque colonie et le chant produit par les individus de cette colonie, nous avons également pu définir une autre unité de chant appelée "core motif" (Figure 1C). Le core motif est défini comme l'unité de chant la plus large qui puisse être comparée au modèle originel. En effet, il se peut que, dans leur motif (l'unité de chant répétée), les mâles aient introduit des syllabes ne faisant pas partie du modèle de chant. Le motif est donc parfois plus large que le core motif (Figure 1C).

Lors de la création de chaque colonie, les mâles fondateurs ont été introduits dans une volière avec des femelles et ont pu se reproduire librement pendant plus d'un an. Pour la colonie A1, nous avions sélectionné 10 mâles fondateurs ayant produit une très bonne imitation du modèle de chant A et nous les avons placés avec 10 femelles. Au bout de 400 jours, 48 mâles ont éclos au sein de cette colonie. Par la suite, nous avons créé la colonie A2 à partir de 3 mâles ayant grandi dans la colonie A1. Après l'installation de ces 3 mâles dans une volière avec 3 femelles, 34 jeunes mâles ont éclos à l'issue d'une période de 400 jours. La colonie B, quant à elle, a été créée à partir de 3 mâles fondateurs ayant produit une très bonne imitation du modèle B et 3 femelles. Après 555 jours, 35 mâles ont éclos au sein de cette colonie. Nous avons donc analysé le chant de tous les mâles de chaque colonie et nous avons également analysé les chants d'un groupe appelé "groupe C" qui correspond à des mâles ayant été élevés dans des volières standard sans aucune tentative de sélection basée sur leurs chant (les jeunes avaient à leur disposition des mâles adultes chantant des chants différents). Ce groupe C est constitué de 24 individus du même patrimoine génétique que les oiseaux de nos trois colonies.

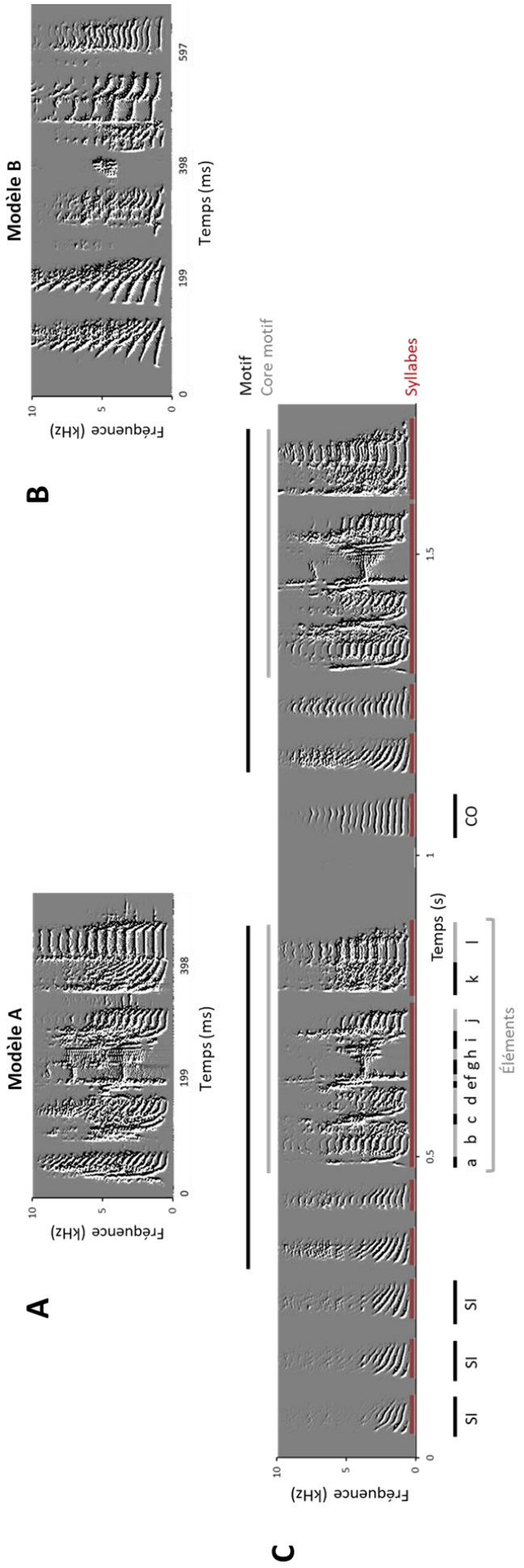

Figure 1 : Spectrogrammes de chants de diamant mandarin. (A) Modèle de chant A. (B) Modèle de chant B. (C) Représentation des différentes unités constituant une phrase de chant : les syllabes sont soulignées en rouge, les core motifs sont indiqués par les barres grises et les motifs par les barres noires. "SI" signifie "Syllabes Introductives", et "CO" signifie "Connecteur". Les lettres minuscules de *a* à *l* représentent les différents éléments d'un core motif.

Le premier but de l'étude était de déterminer si les mâles éclos au sein des trois colonies s'étaient conformés au modèle de chant ou bien avaient dévié de celui-ci. Nous avons donc focalisé notre analyse sur le core motif et, à l'aide d'une procédure semi automatisée, nous avons calculé un score de similarité entre le core motif de chaque mâle et le modèle de chant de sa colonie. Nous avons observé une certaine variabilité interindividuelle dans les scores de similarité : certains mâles avaient produit une très bonne copie du modèle de chant et d'autres une moins bonne. Malgré cette variabilité, dans la colonie A1, la plupart des mâles avaient produit une très bonne imitation du modèle de chant. Nous avons trouvé les mêmes résultats dans la colonie A2 et dans la colonie B. De plus, même des jeunes ayant éclos tardivement (après plusieurs générations) avaient un core motif très similaire à leur modèle de chant. Autre résultat important : dans l'ensemble, la similarité avec le modèle de chant diminuait avec le temps dans les trois colonies. Cela indiquait donc que le core motif changeait au cours du temps, dans les trois colonies.

Après nous être intéressés au core motif, nous avons ensuite focalisé notre analyse sur la phrase de chant, une unité beaucoup moins étudiée que le motif dans les études sur le chant du diamant mandarin. Nous avons ainsi segmenté les phrases de chant en syllabes et ce pour plusieurs phrases de chant pour chaque mâle, afin d'obtenir une base de données de 300 syllabes par mâle. Nous avons ensuite pu classifier toutes ces syllabes en trois catégories : 1) syllabe introductive ; 2) connecteur ; 3) syllabe du motif. Comme premier indicateur de la structure de la phrase de chant, nous avons mesuré le nombre de types de connecteurs produits par chaque mâle. Dans les trois colonies, nous avons ainsi observé une grande variabilité interindividuelle dans le nombre moyen de types de connecteurs produits par phrase de chant pour chaque mâle : certains oiseaux n'utilisaient aucun connecteur entre deux motifs, alors que d'autres produisaient plusieurs types de connecteurs par phrase de chant, et ce, dans les trois colonies. De par le nombre réduit de mâles fondateurs dans la colonie A2 et B, nous en avons déduit que

cette variabilité ne pouvait pas provenir uniquement de la variabilité préexistante dans le chant des fondateurs. En outre, ce résultat ne pouvait pas être inhérent au modèle de chant puisque les mêmes résultats ont été trouvés dans les colonies chantant le modèle A et dans la colonie B. Puisque de la variabilité était apparue dans la structure de la phrase de chant des oiseaux des trois colonies, la présence de ces connecteurs aurait pu influencer le degré de stéréotypie du chant. Nous nous sommes donc intéressés à d'autres indicateurs de la structure de la phrase de chant en quantifiant la stéréotypie des phrases de chant de chaque mâle via trois mesures bien établies : le score de linéarité, de cohérence et de stéréotypie de la phrase de chant. Cependant, nous n'avons observé aucun changement significatif de ces mesures au cours du temps dans nos trois colonies.

Après avoir étudié le niveau macrostructural de l'organisation du chant, nous avons focalisé nos analyses sur le niveau syllabique et subsyllabique (le niveau des "éléments"). En calculant la durée moyenne des syllabes sur 300 syllabes par mâle, nous avons pu observer une diminution de la durée des syllabes au cours du temps dans la colonie A1 mais pas dans la colonie A2 ni B. Cela indiquerait donc que le processus d'évolution du chant au cours du temps (d'abord perçu au niveau du core motif) n'a pas eu le même impact sur les syllabes des trois colonies. Comme mentionné précédemment, les syllabes peuvent être subdivisées en unités fines appelées "éléments". En repérant des changements abrupts dans l'amplitude ou l'entropie du chant, nous avons donc pu segmenter en éléments les syllabes constituant le core motif de chaque mâle. Cette segmentation nous a permis d'extraire 13 paramètres acoustiques pour chaque unité segmentée (syllabe ou élément). Afin de vérifier si certains sons pouvaient être spécifiques à une colonie ou à un modèle de chant au niveau syllabique et subsyllabique, nous avons réalisé une analyse de clusters basée sur ces 13 paramètres acoustiques (chaque cluster représentant un type de syllabes ou un type d'éléments particulier). L'analyse de clusters au niveau syllabique a démontré que les colonies A1 et A2 partageaient les mêmes types de

syllabes mais étaient plus éloignées, en termes de répartition de ces types de syllabes, de la colonie B et du groupe C. L'analyse ayant identifié 26 types de syllabes en tout, nous nous sommes aperçus que 9 de ces types de syllabes étaient spécifiques au modèle de chant A (regroupant donc les colonies A1 et A2), 2 de ces types de syllabes étaient exclusivement produits dans la colonie B (donc spécifiques au modèle de chant B) et un seul type de syllabes était spécifique au groupe C. Concernant l'analyse de clusters au niveau subsyllabique, de la même façon, nous avons pu déterminer que les colonies A1 et A2 étaient très proches en termes de répartition de ces types d'éléments, et plus éloignées de la colonie B et du groupe C. Sur les 15 types d'éléments trouvés par l'analyse de clusters, 4 étaient spécifiques au modèle de chant A, un était spécifique au modèle de chant B et aucun au groupe C. Dans leur globalité, ces résultats révèlent que chaque modèle de chant a conduit à l'établissement d'un répertoire spécifique de types de syllabes et d'éléments.

En observant la dynamique d'utilisation de ces clusters au cours du temps dans les colonies, nous nous sommes aperçus que la quasi-totalité des types de syllabes et d'éléments étaient déjà présents dans le répertoire de chants des fondateurs. En calculant le pourcentage de clusters produits par chaque mâle (par rapport au répertoire entier de le colonie), nous nous sommes aperçus d'une grande variabilité interindividuelle dans l'utilisation de ces clusters : certains mâles produisaient un plus grand nombre de types de syllabes et d'éléments que d'autres. Nous avons souhaité voir si ce phénomène était relié au temps : dans la colonie A1, les mâles utilisent de moins en moins de types de syllabes au cours du temps (les mâles ayant éclos tard en utilisent moins que les mâles ayant éclos au début de la fondation de la colonie). Cependant, nous n'avons pas retrouvé ce résultat dans les colonies A2 et B. Comme avec les résultats concernant la durée des syllabes, cela suggère que le processus d'évolution du chant n'a pas eu d'impact au niveau syllabique. En revanche, dans les colonies A1 et A2, nous avons pu observer une diminution significative dans la production des différents types d'éléments au

cours du temps (mais pas dans la colonie B). Cela montre, une fois encore, que le core motif du chant a évolué au fil du temps. Avec les résultats concernant la diminution significative du score de similarité au modèle de chant, cette découverte suggère que le core motif s'est simplifié au cours du temps, les mâles utilisant de moins en moins de types d'éléments. Pour vérifier cette hypothèse de la simplification, nous avons regardé si le nombre absolu d'éléments par core motif changeait au cours du temps. Et en effet, nous avons observé que le nombre d'éléments par core motif diminuait significativement au cours du temps dans nos trois colonies. De plus, le nombre d'éléments par core motif étant grandement corrélé à la durée du core motif, nous avons également observé une diminution significative de la durée du core motif au cours du temps dans les colonies A1 et B. Pour résumer, tous les résultats présentés jusqu'ici suggèrent que des spécificités acoustiques peuvent émerger et être maintenues dans des colonies de diamants mandarins, même si le core motif du chant tend à se simplifier au fil du temps.

Pour finir, nous avons comparé nos 4 groupes d'oiseaux entre eux (les trois colonies et le groupe C) afin de vérifier si le fait d'imposer un modèle de chant influençait l'émergence potentielle de dialectes propres à chaque groupe. En nous basant tout d'abord sur une mesure relative à la variabilité du chant au niveau des 300 syllabes produites par chaque mâle de chaque colonie, nous avons constaté que les oiseaux de la colonie A1 et A2 présentaient la même variabilité de chant mais différaient de la colonie B et du groupe C, la colonie B manifestant une variabilité de chant plus importante que les autres groupes, et le groupe C manifestant une variabilité beaucoup plus faible que dans les trois colonies. Ces résultats suggèrent que, de par leur partage du même modèle de chant, les oiseaux de la colonie A1 et A2 utilisent le même espace acoustique, mais un espace acoustique différent de celui de la colonie B possédant un modèle de chant différent. Enfin, le fait que le groupe C présente une variabilité plus faible que les trois autres colonies suggère que le fait d'imposer un modèle de chant à nos oiseaux les a contraints à introduire plus de variabilité autour de leur core motif afin de pouvoir se distinguer

les uns des autres, entraînant alors une plus grande variabilité du chant. En conclusion, le manque de variabilité dans le modèle de chant imposé dans les trois colonies, semble être un facteur majeur dans la détermination de la variabilité acoustique au sein d'un groupe de diamants mandarins. Cette variabilité acoustique est exprimée au niveau syllabique du chant et peut être utilisée pour différencier les groupes en fonction de leur exposition précoce à un modèle de chant unique.

Jusqu'ici, nos résultats suggèrent que les 4 groupes d'oiseaux diffèrent dans leur utilisation de l'espace acoustique et que chaque modèle de chant détermine un espace acoustique particulier. Mais pour pouvoir confirmer que ces colonies présentent des dialectes de chant différents, nous avons réalisé une analyse discriminante basée sur les 13 paramètres acoustiques du core motif de chaque mâle de nos 4 groupes. Cette analyse d'une grande précision a confirmé que les oiseaux de la colonie A1 et A2 présentent les mêmes spécificités acoustiques au niveau de leur core motif, que les oiseaux de la colonie B eux diffèrent de ceux de la colonie A1 et A2 en termes de spécificités acoustiques du core motif, et que les oiseaux du groupe C partagent des spécificités avec les colonies A1, A2 et B. Une fois de plus, ces résultats suggèrent que la sélection de fondateurs chantant un même modèle de chant dans nos colonies, a conduit à des spécificités acoustiques dans le core motif qui permettent de distinguer avec une grande précision l'origine des oiseaux.

Pour finir, nous avons continué à observer les différences acoustiques entre les 4 groupes au niveau de la structure du chant, au niveau syllabique et subsyllabique : 1) les colonies A1 et A2 ne diffèrent pas en termes de nombre moyen de connecteurs produits par phrase de chant mais diffèrent de la colonie B. Le groupe C, lui, diffère de la colonie A2 à ce niveau. Cela montre que les deux colonies partageant le même modèle de chant sont plus proches entre elles en termes de structure de la phrase de chant, que des autres groupes. 2) En examinant la répartition des intervalles de silence entre les syllabes d'une phrase de chant, nous

avons observé que les deux colonies chantant le même modèle de chant présentaient la même distribution de leurs intervalles inter-syllabiques, mais une répartition différente de celle des autres groupes. 3) Au niveau syllabique, pas de différence entre les groupes dans la durée moyenne de leurs syllabes. 4) Au niveau subsyllabique, les colonies A1 et A2 ne diffèrent pas en termes de nombres d'éléments par core motif mais diffèrent de la colonie B. Comme au niveau de la structure de la phrase de chant, cela montre que les deux colonies possédant le même modèle de chant originel sont plus proches l'une de l'autre sur le plan de l'organisation subsyllabique, que des deux autres groupes.

En complément des analyses acoustiques, dans les colonies A2 et B, nous avons observé et décrit les interactions sociales de tous les mâles durant la phase sensible de leur vie précoce (entre les jours 25 et 65), à raison de plusieurs fois par semaine et par sessions de 10mn par mâle. En effet, il a déjà été montré que les dynamiques de l'apprentissage du chant dépendaient d'interactions sociales avec des congénères. Par exemple, le choix d'un tuteur par un jeune peut être influencé par divers facteurs tels que la quantité de soins parentaux ou le niveau d'agressivité du tuteur. Il a également été démontré que les pairs (oiseaux du même âge) influençaient l'apprentissage vocal via la transmission horizontale et qu'un frère pouvait donc être un aussi bon modèle de chant qu'un adulte. Enfin, comme mentionné plus haut, il a récemment été suggéré que les femelles pouvaient également guider le processus d'apprentissage du chant des jeunes mâles. Nous voulions savoir si de telles interactions sociales allaient avoir un effet sur l'apprentissage du modèle de chant chez les mâles de nos colonies. Nous avons pu observer que dans la colonie B, les jeunes mâles interagissaient autant avec des jeunes femelles, des femelles adultes, des jeunes mâles et des mâles adultes. En revanche, dans la colonie A2, les jeunes mâles interagissaient préférentiellement avec des mâles adultes. Cependant, les individus interagissant davantage avec des mâles adultes ne présentaient pas un meilleur score de similarité au modèle de chant de leur colonie. Bien que les jeunes des deux

colonies avaient, en moyenne, plus d'interactions affiliatives qu'agonistiques avec leurs congénères, ceci n'avait aucun impact sur la similarité de leur chant au modèle. En considérant uniquement les interactions de chaque jeune avec son "interacteur principal" (IP : l'oiseau avec lequel il a le plus interagi durant sa période sensible), nous nous sommes rendu compte que beaucoup d'oiseaux possédaient une femelle comme IP et que ceux qui avaient un mâle en tant qu'IP ne démontraient pas un meilleur score de similarité au modèle de chant. Enfin, en nous focalisant uniquement sur les interactions avec le mâle IP, nous n'avons trouvé aucun lien significatif entre les interactions sociales partagées avec cet individu et les paramètres du chant (similarité au modèle de chant ou même similarité au chant du male IP). Ces observations sociales montrent donc que, durant la phase sensible d'apprentissage du chant, les jeunes mâles interagissent avec tout type de congénères et pas préférentiellement avec des mâles adultes, et que le degré ou la nature des interactions avec des mâles ne sont pas des indicateurs fiables de l'apprentissage du chant chez les jeunes mâles de nos colonies.

En conclusion, les résultats de cette première étude démontrent que des dialectes de chants peuvent émerger chez le diamant mandarin en conditions contrôlées de laboratoire, contrairement à ce qui a été suggéré par d'autres études. En outre, les spécificités acoustiques propres à chaque dialecte se retrouvent à divers niveaux structurels du chant du diamant mandarin. Nos résultats révèlent une certaine conformité entre les individus d'une même colonie au niveau du core motif. Cela n'empêche pas d'observer une légère évolution de cette unité de chant au cours du temps et le processus de simplification du core motif pourrait être comparé à des processus similaires ayant été observés dans l'évolution du langage : il a été démontré qu'un comportement transmis culturellement, allait avoir tendance à évoluer afin de maximiser sa propre transmission, en devenant de plus en plus structuré et facile à apprendre. Par ailleurs, nos résultats sont une invitation à prendre systématiquement en compte la phrase de chant qui a été sous-estimée dans les études de chant chez le diamant mandarin. En effet, bien que les

individus se soient conformés au modèle de chant au niveau de leur core motif, ils ont été capables d'introduire de la variabilité autour de celui-ci, via l'utilisation de divers connecteurs dans leurs phrases de chant. Ils ont ainsi pu diverger du modèle originel, ce qui pourrait faciliter la reconnaissance individuelle et la coordination entre individus lors d'interaction vocales. Au travers de nos résultats, il apparaît donc que l'évolution culturelle peut moduler le chant d'oiseau à différentes échelles. Contrairement à nos prédictions, nos résultats indiquent plutôt que la conformité et la variabilité ne sont pas exclusives et qu'elles s'expriment chacune dans différentes unités du chant et de manière complémentaire, sans empêcher l'émergence et la stabilité de dialectes artificiels. Nos résultats suivent le mécanisme de balance entre les forces sociales convergentes et divergentes, proposé par certains auteurs : l'imitation et l'innovation (ou les erreurs de copies) s'observent toutes deux au sein de nos colonies et fonctionnent de manière complémentaire pour façonner la culture vocale observée dans chacune de nos colonies. Dans ce contexte, on peut donc dire que les dialectes artificiels de chant chez le diamant mandarin peuvent être considérés comme une culture vocale polymorphique stable.

Pour finir, dans notre étude, nous n'avons pas été à même d'identifier un pattern clair entre des facteurs sociaux et la capacité des mâles à produire une bonne imitation du modèle de chant. A l'opposé, nos observations comportementales suggèrent plutôt que l'apprentissage du chant chez le diamant mandarin est modulé par des interactions sociales diverses avec des individus qui ne sont pas nécessairement des mâles adultes. Puisque les jeunes mâles étaient à même d'interagir autant avec des mâles qu'avec des femelles, il est très probable que des feedbacks de ces deux catégories de congénères aient influencé leur apprentissage du chant et donc l'établissement des dialectes. Puisque les dialectes jouent un rôle dans la sélection sexuelle et constituent potentiellement une signature de groupe chez les espèces sociales, la découverte de dialectes chez le diamant mandarin ouvre de nouvelles perspectives de recherche pouvant

permettre de consolider cette espèce comme modèle de choix pour évaluer les aspects proximaux et ultimes de l'apprentissage vocal.

Chapitre 2 : La préférence des femelles pour le dialecte de leur colonie

Dans le chapitre 2, je présente une étude destinée à évaluer la préférence des femelles diamant mandarin pour les dialectes de chants créés artificiellement. Comme mentionné précédemment, il est établi que les femelles de cette espèce expriment une préférence pour les chants entendus durant leur vie précoce. En raison des conditions artificielles que nous avons établies pour étudier l'émergence des dialectes de chant, les femelles de nos colonies n'ont pu entendre que les chants produits par les mâles de leur propre colonie lorsqu'elles étaient jeunes. Chez d'autres espèces, il a été démontré que les dialectes de chant pouvaient influencer les préférences d'appariement des femelles, celles-ci montrant une préférence pour le chant de mâles de leur propre dialecte. Ce phénomène pourrait également influencer la stabilité des dialectes. C'est pour ces raisons que nous nous sommes demandé s'il existait un lien entre la préférence des femelles et les dialectes de chant chez le diamant mandarin. Notre prédiction était que les femelles allaient préférer les chants ressemblant à ceux des mâles de leur propre colonie.

Pour tester la préférence des femelles, nous avons utilisé une tâche de conditionnement opérant avec du chant en guise de récompense. Cette méthode a prouvé son efficacité dans l'évaluation des préférences des femelles, chez le diamant mandarin mais aussi d'autres espèces comme le canari (*Serinus canaria*). Le dispositif consiste en une cage placée dans un caisson d'isolation acoustique et dans laquelle se trouvent deux perchoirs ; au-dessus de chaque perchoir se trouve une clé de couleur rouge qui déclenche la diffusion d'un chant lorsque la femelle appuie dessus (Figure 2A). A chaque fois qu'une femelle appuie sur une clé, l'ordinateur enregistre cet appui et indique le chant correspondant, ce qui nous permet de suivre la réponse

de la femelle au jour le jour. Une webcam placée dans le caisson nous permettait de surveiller l'activité de la femelle durant le test (Figure 2A).

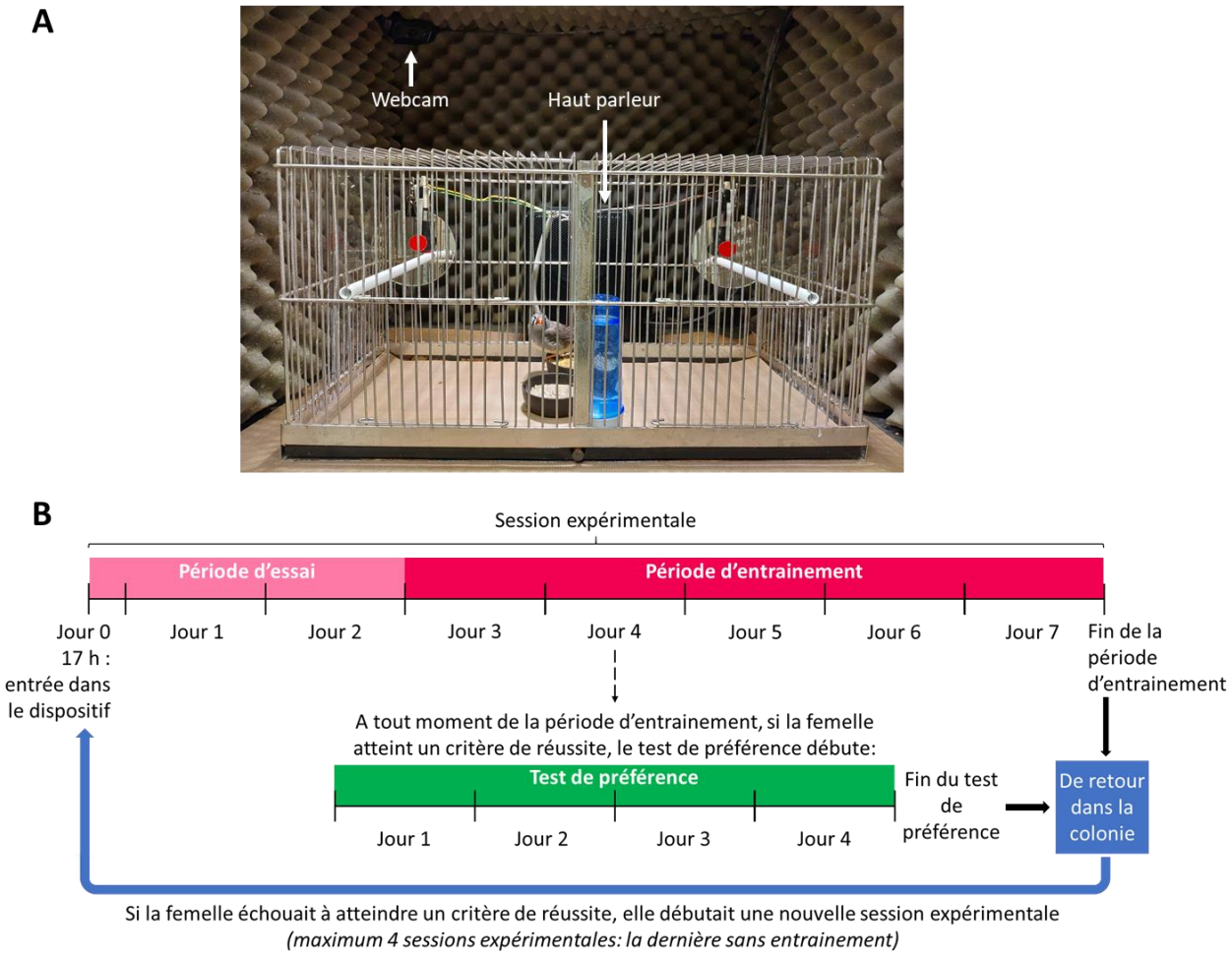

Figure 2 : Dispositif expérimental et déroulé de l'expérience. (A) Dispositif expérimental pour le test de préférence. (B) Déroulé de la procédure expérimentale pour toutes les femelles, hébergées dans la volière de leur colonie avant d'être placées en caisson d'isolation acoustique, au début de la session expérimentale.

Durant le test, chaque femelle avait la possibilité de déclencher deux types de chants : une des clés déclenchait le playback d'un chant similaire au type de chant produit dans la colonie de la femelle, qu'on appellera par la suite "CST" (Colony Song Type) ; et l'autre clé déclenchait le playback d'un chant de congénère mais différent du type de chant de la colonie de la femelle, qu'on appellera "N-CST" (Non-Colony Song Type). Pour éviter un potentiel effet de familiarité,

chacun des deux types de chant étaient produits par un mâle non familier. Puisque les mâles des colonies A1 et A2 chantent le même type de chant, le CST d'une femelle A1 était un chant produit par un mâle de la colonie A2 et vice-versa. Les mâles de la colonie B produisant un type de chant différent, le CST diffusé aux femelles de la colonie B était un chant produit par un mâle originellement entraîné à produire une bonne imitation du modèle de chant B mais qui n'avait pas été sélectionné pour être fondateur de la colonie B. Les N-CST des femelles des trois colonies étaient des chants produits par des oiseaux provenant du pool général d'oiseaux de l'Institut Max Planck, à Seewiesen, en Allemagne.

Pour créer les stimuli, nous avons sélectionné des chants produits naturellement par des mâles en caisson, et pour les CST, uniquement des mâles ayant produit un chant très similaire au modèle originel de la colonie. Afin d'uniformiser les stimuli allant être présentés aux différentes femelles, une phrase de chant naturelle était sélectionnée puis modifiée digitalement de manière à obtenir des chants de durées similaires et reproduisant les caractéristiques d'un chant naturellement dirigé vers une femelle, c’est-à-dire un chant "dirigé" très stéréotypé. Nous avons donc, pour chaque stimulus, conservé les 4 premières syllabes introductives, suivies par 4 répétitions du motif. Afin d'éviter la pseudo-réplication, nous avons créé 10 sets de stimuli uniques, et chaque femelle se voyait attribuer un set spécifique lors du test.

Le déroulement du test de préférence est le suivant : chaque femelle était capturée dans sa colonie et placée dans le dispositif aux alentours de 17h (jour 0 de l'expérience). A partir de ce moment, la femelle pouvait accéder aux deux clés et déclencher les chants. Les femelles devant d'abord apprendre comment appuyer sur les clés, la première session expérimentale débutait par une période d'essai de deux jours (jour 1 et 2 de l'expérience). Nous avions fixé deux critères d'apprentissage : on considérait qu'une femelle avait appris avec succès comment appuyer sur les clés si 1) elle réalisait 10 appuis sur chaque clé dans la même journée, ou si 2) elle réalisait au moins 20 appuis sur la même clé dans le cas des femelles ayant appuyé

exclusivement sur une des deux clés. Le jour où un de ces deux critères était atteint était considéré comme le jour 1 du test de préférence. Suivant le jour 1, la femelle pouvait interagir librement avec les clés pour les trois jours suivants (jour 2, 3 et 4 du test de préférence). A la fin du jour 4, la femelle était replacée dans sa colonie. Le test de préférence durait donc 4 jours, avec un changement de côté des stimuli chaque nuit, pour éviter un biais de côté : deux jours avec le CST déclenché par la clé droite et deux jours avec le CST déclenché par la clé gauche.

Les femelles n'ayant pas réussi à appuyer régulièrement sur les clés à la fin de la période d'essai suivaient une période d'entraînement (du jour 3 au jour 7 de l'expérience), pendant laquelle l'attention de la femelle était attirée vers les clés à l'aide d'appuis réalisés par l'expérimentateur, de graines ou de matériel de construction du nid scotché aux clés. Si, à l'issue des 7 jours d'expérience, la femelle n'avait toujours pas réussi à appuyer régulièrement sur les clés, elle était replacée dans sa colonie pour une pause d'une semaine minimum avant de débuter une deuxième session expérimentale qui se déroulait de la même manière. Au maximum, une femelle pouvait subir 4 sessions expérimentales (sachant que lors de la quatrième, aucun entraînement n'était réalisé, laissant une dernière opportunité à la femelle d'apprendre spontanément à appuyer sur les clés). Si, à l'issue de la 4ième session, la femelle n'avait toujours pas appris comment appuyer sur les clés, nous considérions qu'elle avait échoué à l'expérience. La totalité de la procédure expérimentale est représentée dans la Figure 2B.

En tout, 63 femelles ont été testées mais seules 37 ont réussi à atteindre un des deux critères d'apprentissage : 10 dans la colonie A1, 11 dans la colonie A2 et 16 dans la colonie B. Afin d'analyser la préférence des femelles, nous avons calculé leur ratio de préférence pour le chant de leur colonie (CST) : nombre total d'appuis réalisés pour déclencher le CST durant les 4 jours de test, divisé par le nombre total d'appuis réalisés sur les deux clés. Nous avons ensuite évalué si leur ratio de préférence était significativement différent du niveau de chance de 0,5.

Le principal résultat de cette étude est, qu'au niveau individuel, la grande majorité des femelles des trois colonies ont montré une préférence significative pour le CST (le chant de leur colonie) comparé au N-CST (un chant différent du type de chant de leur colonie). Cependant, cette préférence n'était pas reflétée au niveau du groupe dans les trois colonies : la préférence significative pour le CST au niveau du groupe n'a été observée que dans la colonie A2. Le nombre absolu d'appuis réalisés lors des 4 jours de test variait grandement entre les femelles. Afin d'évaluer un effet potentiel de la motivation sur les ratios de préférence observés, nous avons mesuré la force de la préférence de chaque femelle, en divisant le nombre d'appuis réalisés pour le type de chant préféré par le nombre d'appuis pour le chant non préféré. Finalement, nous n'avons trouvé aucune corrélation significative entre le nombre total d'appuis réalisés et la force de la préférence, dans aucune des trois colonies. La préférence des femelles n'était donc pas due à leur niveau de motivation.

Nous avons ensuite regardé s'il existait des différences entre les trois colonies au niveau des deux mesures principales : le ratio de préférence pour le CST et le nombre total d'appuis réalisés. Le ratio de préférence pour le CST était plus élevé dans la colonie A1 que dans la colonie B mais il n'y avait aucune différence entre les autres colonies. De manière similaire, les femelles de la colonie A1 avaient significativement réalisé plus d'appuis que les femelles de la colonie B, mais il n'y avait aucune différence dans cette mesure entre les autres colonies. Le nombre de sessions expérimentales nécessaires pour réussir le test n'avait aucun impact sur ces deux mesures comportementales.

Les résultats de cette expérience vont dans le même sens que plusieurs études précédentes ayant démontré que les femelles diamant mandarin préfèrent les chants qu'elles ont entendus lorsqu'elles étaient jeunes (dans notre cas, le dialecte de chant de leur propre colonie). Cependant, cette étude se démarque des autres études sur le sujet de la préférence des femelles, puisque ces études donnent généralement le choix aux femelles entre le chant d'un individu

familier (souvent le père ou le tuteur) et le chant d'un individu non familier. Ici, le fait que nos femelles préfèrent le CST par rapport au N-CST, même si ces deux chants sont chantés par des individus non familiers, suggère que la préférence apprise lors de la vie précoce est suffisamment forte pour être généralisée à un émetteur non familier (ce qui a déjà été démontré dans d'autres études). De plus, cette préférence ne dépend pas du dialecte de chant (A ou B), puisque, dans les trois colonies, les femelles ont démontré une préférence pour le CST.

Puisque, comme mentionné précédemment, la préférence des femelles pour le dialecte natal pourrait influencer la stabilité de celui-ci, et que les femelles guident potentiellement le processus d'apprentissage du chant des jeunes mâles via un feedback social, il est logique de penser que les préférences des femelles diamant mandarin ont eu un rôle déterminant dans l'établissement et la stabilité des dialectes de chant artificiels dans nos trois colonies. Plus spécifiquement, la préférence des femelles pour le CST (très similaire au modèle de chant originel), aurait pu influencer les jeunes mâles à se conformer à ce type de chant.

Les femelles de nos colonies ayant pu interagir librement avec les mâles durant toute leur vie, contrairement aux études classiques sur le diamant mandarin, il est probable que certaines femelles se soient appariées et aient déjà participé à la reproduction avant d'être testées. Comme nous n'avons pas pu contrôler ce facteur, il est possible que les quelques femelles n'ayant pas démontré de préférence significative pour le CST soient des femelles qui se sont appariées à des mâles produisant une mauvaise copie du type de chant de la colonie.

Malgré la préférence individuelle de la plupart des femelles pour le CST, cette préférence ne se reflétait pas au niveau du groupe dans les trois colonies De plus, certaines femelles ont démontré une préférence pour le N-CST. Chez d'autres espèces comme le canari, les femelles montrent des préférences claires pour certaines caractéristiques de chant. Bien que, chez le diamant mandarin, de telles préférences pour des types de sons spécifiques n'aient pas été démontrées, nous ne pouvons exclure le fait que certaines caractéristiques acoustiques des

stimuli de N-CST aient pu être préférées par quelques femelles, influençant alors la préférence globale au niveau du groupe.

Enfin, le fait que les femelles de A1 aient démontré une préférence plus forte pour le CST et aient plus appuyé sur les clés que les femelles de la colonie B, ne peut pas être expliqué par la nature du dialecte (A ou B), puisqu'aucune différence n'a été observée entre les colonies A2 et B. Cependant, certains chercheurs ont prouvé que l'expérience des femelles à l'âge adulte pouvait influencer leurs préférences de chant. Ainsi, nous pouvons supposer que l'expérience de nos femelles au sein de leur colonies respectives (c'est-à-dire leur exposition au type de chant de la colonie et la capacité des femelles à interagir librement avec les mâles) a influencé leur préférence pour le CST et leur motivation à l'entendre. En effet, lors du test, les femelles de A1 étaient beaucoup plus âgées que les femelles de B. Aussi avaient-elles plus d'expérience avec le dialecte de leur colonie, ce qui aurait pu entraîner une préférence plus forte pour celui-ci et une plus grande motivation à l'écouter.

Chez les diamants mandarins, le manque de saisonnalité dans la reproduction soulève des problèmes concernant la nature des préférences observées chez les femelles. En effet, dans notre étude nous n'avons pas testé la réceptivité sexuelle des femelles. Aussi pouvons-nous nous demander si la préférence pour le CST est une préférence sexuelle reliée au choix de partenaire ou bien une préférence sociale. En effet, chez les espèces sociales, le fait de partager un même type de chant peut influencer la cohésion du groupe. Dans ce contexte, le chant pourrait alors être interprété comme un signal affiliatif plutôt qu'un signal sexuel, chez cette espèce sociale qu'est le diamant mandarin.

Pour conclure, notre étude démontre avec succès que les femelles expriment une préférence pour le chant qu'elles ont entendu durant leur vie précoce mais elle est la première à démontrer un lien direct entre les dialectes de chant et la préférence des femelles chez le diamant mandarin. Nos résultats soulèvent également la difficulté d'évaluer la nature des préférences

des femelles de cette espèce mais ils ouvrent la voie pour vérifier si les dialectes de chant peuvent être utilisés comme un signal affiliatif.

Chapitre 3 : Le chant, un médiateur pour l'apprentissage social ?

Dans ce 3ème et dernier chapitre, je me suis intéressée au chant en tant que signature de groupe pouvant jouer un rôle dans l'apprentissage social chez le diamant mandarin. Il a été montré que les dialectes de chant pouvaient signaler l'identité du groupe et potentiellement renforcer la cohésion sociale au sein de groupes d'oiseaux issus d'espèces sociales, telle que l'Étourneau sansonnet (*Sturnus vulgaris*). Cette question n'a pas encore été examinée chez le diamant mandarin, et, comme il s'agit également d'une espèce très sociale, l'apprentissage social de choix de nourriture apparaît comme une stratégie adaptative chez cette espèce (par exemple, afin d'éviter une source de nourriture potentiellement toxique). En effet, en utilisant un paradigme classique d'observateur-démonstrateur, plusieurs études ont déjà démontré que les diamants mandarins étaient capables d'apprentissage social d'une tâche de fourragement. De ce fait, cette espèce constitue le modèle parfait pour évaluer les facteurs pouvant affecter les préférences d'apprentissage social. Plusieurs facteurs ont déjà été testés, tels que le sexe, la familiarité et l'environnement postnatal. Cependant, aucune étude ne s'est intéressée à l'effet du chant sur l'apprentissage social. Aussi, en utilisant une méthode similaire à celle des études réalisées sur le sujet de l'apprentissage social, voulions-nous voir si des observateurs mâles et femelles seraient plus à même de copier le choix de nourriture d'un individu chantant le dialecte de chant de leur colonie, ou bien un type de chant différent. Si le chant représente réellement une signature de groupe chez cette espèce, nous prédisons que les oiseaux des deux sexes devraient apprendre préférentiellement d'un démonstrateur chantant leur propre dialecte, et ce, dans chacune de nos trois colonies.

Cette expérience a été conduite dans des caissons d'isolation acoustique. Deux cages étaient placées dans le caisson : une cage pour l'observateur et une cage divisée en deux, pour

les deux démonstrateurs. Chaque oiseau pouvait accéder à deux perchoirs sur lesquels se trouvaient deux mangeoires transparentes. Au sein d'un caisson, nous placions une triade d'oiseaux constituée d'un observateur (mâle ou femelle) et de deux démonstrateurs (mâles). Ainsi, chaque observateur pouvait regarder deux démonstrateurs se nourrir : un démonstrateur chantant le dialecte de sa colonie (appelé démonstrateur "SIM" = similaire) et un démonstrateur chantant un dialecte de chant différent de celui de la colonie de l'observateur (appelé démonstrateur "DIFF" = différent). Les observateurs de la colonie B étaient nécessairement familiers avec leur démonstrateur SIM, puisqu'une seule de nos colonies chantait le dialecte B (le démonstrateur SIM provenait donc forcément de la colonie B). Le Tableau 1 résume les trois triades d'oiseaux possibles au sein du dispositif expérimental et le nombre d'observateurs testés dans chaque colonie.

Tableau 1 : Les trois triades possibles au sein d'un caisson d'isolation acoustique et effectifs. SIM : démonstrateur avec le même dialecte de chant que l'observateur ; DIFF : démonstrateur avec un dialecte de chant différent de celui de l'observateur.

Colonie de l'observateur	n	Familiarité de l'observateur aux démonstrateurs	Colonie du démonstrateur SIM	Colonie du démonstrateur DIFF
A1	12 mâles 9 femelles	Non familier	A2	B
A2	10 mâles 19 femelles	Non familier	A1	B
B	20 mâles 36 femelles	Familier avec le démonstrateur SIM	B	A1 ou A2

Le test d'apprentissage social était composé de 4 phases (Figure 3A). La 1ère phase est la phase d'habituation des démonstrateurs (Figure 3A). Deux démonstrateurs (un oiseau de la colonie A1 ou A2 et un oiseau de la colonie B) sont placés dans la cage des démonstrateurs,

chacun dans une demi-cage. Chaque démonstrateur avait à sa disposition deux mangeoires : une remplie avec des graines jaunes et une avec des graines vertes. Cependant, seule une de ces deux mangeoires était réellement accessible, l'autre étant bloquée à l'aide film plastique. Si le démonstrateur SIM avait accès aux graines jaunes, le démonstrateur DIFF avait accès aux graines vertes et inversement (Figure 3A). Chaque jour, l'activité de chant des deux démonstrateurs était enregistrée et une fois que chacun des deux démonstrateurs avait chanté un minimum de 10 phrases de chants entre 8h et 10h, on considérait alors que l'activité de chant était suffisante et on passait à la deuxième phase du test.

La 2ème phase est la phase d'exposition de l'observateur aux démonstrateurs (Figure 3A). Les mangeoires des démonstrateurs contenant des graines colorées sont remplacées par des graines normales, afin que l'observateur ne soit pas exposé au nouveau type de nourriture avant le test (Figure 3A). L'observateur (mâle ou femelle) est placé dans la cage faisant face aux deux démonstrateurs et peut également accéder à deux mangeoires remplies de graines normales (Figure 3A). Le test d'apprentissage social ne pouvait débuter que lorsque l'observateur avait été suffisamment exposé au chant des deux démonstrateurs. Ainsi, le jour suivant l'introduction de l'observateur dans le dispositif, si les deux démonstrateurs avaient chanté chacun un minimum de 10 phrases de chant le matin entre 8h et 10h, en présence de l'observateur, la troisième phase pouvait commencer (voir ci-dessous). Sinon, les trois oiseaux étaient laissés ensemble pour un maximum de 3 jours, jusqu'à ce que ce critère soit atteint.

La 3ème et 4ème phase constituent les deux phases du test d'apprentissage social en lui-même. La 3ème phase est la phase de démonstration (Figure 3A). Les oiseaux étaient privés de nourriture à 10h et à 15h, puis la phase de démonstration débutait et durait 1h. Les deux démonstrateurs étaient isolés visuellement l'un de l'autre par un panneau opaque (Figure 3A). Dans la demi-cage de chaque démonstrateur, nous placions les deux mangeoires contenant deux couleurs de graines différentes, mais une seule des deux était accessible à l'oiseau (comme dans

la 1ère phase) (Figure 3A). Ainsi, l'observateur pouvait observer chaque démonstrateur se nourrir exclusivement d'une couleur de graines. A la fin de la démonstration, l'observateur était isolé visuellement des démonstrateurs (à 16h) et la phase de test (4ème phase) débutait. Dans cette phase de test, deux mangeoires accessibles étaient placées dans la cage de l'observateur : une contenant des graines jaunes et l'autre des graines vertes (Figure 3A & 3B). Le test durait 1h. A la fin du test, si l'observateur était un mâle, il devenait alors démonstrateur et débutait une phase d'habituation. Le déroulement de l'expérience entière est représenté dans la Figure 3C.

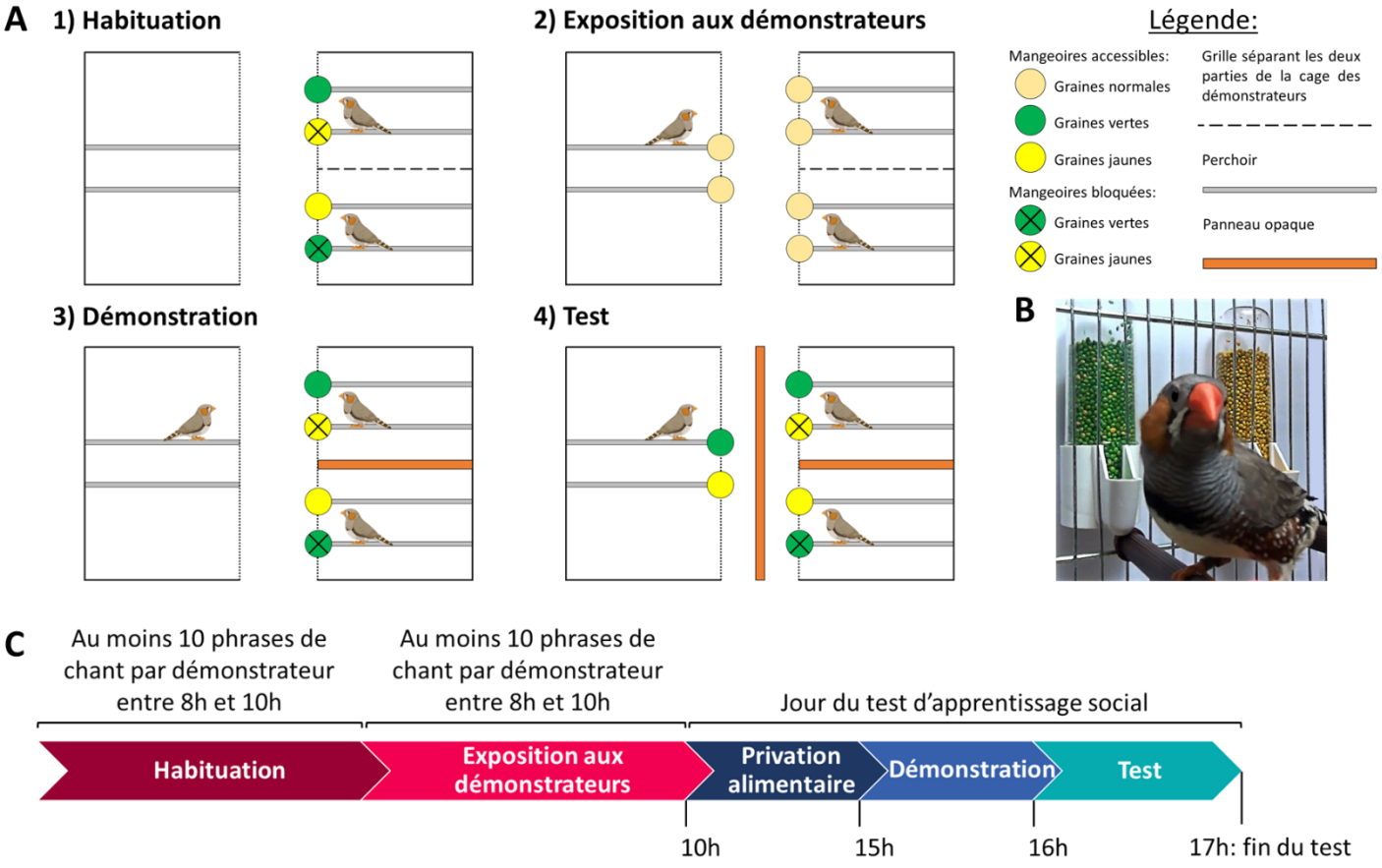

Figure 3 : Dispositif expérimental et déroulé de l'expérience. (A) Vue du haut du dispositif expérimental lors des 4 phases de l'expérience d'apprentissage social. La cage de l'observateur est sur la gauche et celle des démonstrateurs sur la droite. (B) Photo d'un mâle observateur devant les deux mangeoires contenant des graines colorées. (C) Déroulé de la procédure expérimentale avec les différentes phases.

Sur les 42 mâles et 64 femelles testés, 36 mâles et 56 femelles ont été conservés pour analyse. Grâce aux analyses vidéo, nous avons quantifié le nombre de graines ingérées par l'observateur et différencié s'il s'agissait d'une graine de la même couleur que celle consommée par le démonstrateur SIM ("graine SIM"), ou de la même couleur que celle consommée par le démonstrateur DIFF ("graine DIFF"). Nous avons également codé le nombre de graines ingérées par chaque démonstrateur (qui ne pouvait consommer qu'un type de graines). Enfin, nous avons quantifié l'activité de chant des deux démonstrateurs durant la durée totale d'exposition de l'observateur à ces démonstrateurs, en comptant le nombre de motifs produits.

Ayant observé les mêmes résultats en analysant l'activité alimentaire des observateurs durant les 15 premières minutes du test et durant l'heure entière, nous avons choisi de présenter uniquement les résultats concernant les 15 première minutes de test. Tout d'abord, nous avons pu observer que les observateurs, qu'ils soient mâles ou femelles, n'étaient pas sélectif envers un type de graines en particulier : il n'y a pas significativement plus d'observateurs ayant ingéré préférentiellement des graines SIM que d'observateurs ayant ingéré préférentiellement des graines DIFF. Nous avons également testé si la médiane du ratio de préférence des observateurs pour les graines SIM (nombre de graines SIM ingérées, divisé par le nombre total de graines ingérées), était significativement différente du niveau de hasard de 0,5. Ce ne fut pas le cas, ni pour les femelles, ni pour les mâles, indiquant que les observateurs n'ont pas appris préférentiellement du démonstrateur SIM plutôt que du démonstrateur DIFF. Dans leur globalité, ces résultats indiquent qu'il n'y a pas de copie de choix de nourriture par rapport au démonstrateur SIM.

Puisque les observateurs de la colonie B étaient familiers à leur démonstrateur SIM, nous nous sommes appliqués à savoir si cette familiarité avait un effet sur la propension de l'observateur à copier le choix de nourriture de ce démonstrateur. Cependant, nous n'avons trouvé aucun effet significatif de la familiarité sur la réponse de l'observateur, indiquant que la

proportion de graines SIM ingérées ne différait pas, selon que le démonstrateur SIM était familier ou non à l'observateur.

Puisque ni le type de chant chanté par les démonstrateurs (correspondant soit au dialecte de la colonie de l'observateur, soit à un dialecte différent), ni la familiarité avec le démonstrateur SIM, ne semblaient influencer le choix de nourriture de l'observateur, nous avons également testé d'autres effets potentiels du comportement des démonstrateurs sur la réponse de l'observateur : l'effet de l'activité de chant et de l'activité alimentaire. Ni chez les femelles, ni chez les mâles observateurs, nous n'avons trouvé de différence significative de la médiane du ratio de préférence pour le démonstrateur chantant le plus, par rapport au niveau de hasard de 0,5. Cela suggère donc que les observateurs n'ont pas préférentiellement copié le choix de nourriture du démonstrateur qui chantait le plus, comparé au démonstrateur qui chantait le moins. Concernant l'effet de l'activité alimentaire, nous n'avons pas non plus trouvé de différence significative par rapport à 0,5 dans la médiane du ratio de préférence pour le démonstrateur mangeant le plus ; ni chez les mâles, ni chez les femelles. Cela indique donc que les observateurs n'ont pas préférentiellement copié le choix de nourriture du démonstrateur qui se nourrissait le plus lors de la démonstration, comparé au démonstrateur qui mangeait le moins.

Dans leur globalité, les résultats de notre étude ne nous permettent pas de valider notre prédiction qui consistait à dire que les diamants mandarins allaient apprendre préférentiellement d'un individu chantant le dialecte de leur propre colonie, plutôt que d'un individu chantant un dialecte différent. Nous ne pouvons donc pas valider le fait que le chant puisse constituer une signature de groupe jouant un rôle de signal d'affiliation dans une tâche d'apprentissage social en contexte alimentaire. L'absence de résultats concernant l'effet de familiarité entre en contradiction avec une étude précédente ayant démontré qu'un diamant mandarin préférait la nourriture ayant été ingérée par un individu familier. Enfin, contrairement à des études ayant démontré l'effet du sexe de l'observateur dans une tâche d'apprentissage social, nous avons

trouvé les mêmes résultats concernant les femelles et les mâles observateurs, suggérant donc qu'il n'y avait pas d'effet du sexe sur la copie de choix de nourriture.

Plusieurs hypothèses sont proposées quant à l'absence d'apprentissage social dans ce test de copie de choix de nourriture. Tout d'abord, une durée de privation alimentaire trop longue aurait pu amener les observateurs à exprimer un comportement alimentaire davantage motivé par la faim que par un choix social. Ensuite, chez les diamants mandarins, il a été démontré que le recours à des informations sociales lors de la recherche de nourriture variait considérablement entre les individus. Dans ce contexte, il se peut que certains individus aient eu plus tendance à utiliser des informations personnelles pour se nourrir et ne se fiaient donc pas aux informations sociales pouvant être fournies par les démonstrateurs. Un tel comportement pourrait alors avoir caché les préférences sociales d'autres individus au niveau de la population. De plus, notre expérience a permis aux deux démonstrateurs de s’alimenter à partir d’une source de nourriture mangeable, peu importe sa couleur. Ainsi, le comportement des démonstrateurs n'a pas changé après l'ingestion des graines, contrairement à ce à quoi on pourrait s'attendre après l'ingestion d'un aliment toxique ou désagréable. Comme les observateurs ont observé le comportement alimentaire des démonstrateurs pendant une heure, on peut penser que, même si un observateur réussissait à faire la distinction entre les deux dialectes de chant, il / elle n'utilisait pas cette information pour guider son choix alimentaire, car les deux sources de nourriture semblaient fiables. Enfin, il se peut que certains démonstrateurs SIM produisaient de mauvaises imitations du dialecte de chant de leur colonie, ce qui aurait pu induire en erreur l'observateur et l'empêcher d'identifier le chant de ce démonstrateur comme un chant faisant partie du dialecte de la colonie.

Pour finir, nous pouvons émettre différentes hypothèses quant aux facteurs supplémentaires ayant pu influencer la réponse des observateurs, tels que des effets de dominance entre les individus d'une triade ou au contraire, des affinités ; des effets de préférences sexuelles des femelles pour des mâles particuliers, basées sur des critères de chant

mais aussi des critères morphologiques ou de parades sexuelles ; ou encore des effets de traits de personnalité des oiseaux testés.

Suite à nos résultats, il nous paraît important de proposer des méthodes alternatives pour tester l'apprentissage social chez cette espèce, puisque l'utilisation de démonstrateurs réels ne nous as pas permis de distinguer l'effet du dialecte de chant des autres caractéristiques des démonstrateurs, ce qui rend difficile le contrôle de tous les facteurs susceptibles d'affecter la réponse de l'observateur. Ainsi, l'utilisation de démonstrateurs robots, de vidéos ou encore de tests en conditions plus naturelles, pourraient constituer des méthodes expérimentales utiles pour l'évaluation du chant en tant que marqueur de groupe, dans une tâche d'apprentissage social chez le diamant mandarin.

Pour conclure, notre étude a été la première à examiner le rôle des dialectes de chant en tant que signature de groupe dans l'apprentissage social chez les diamants mandarins. Et bien que nos résultats n'appuient pas l'hypothèse que le chant puisse constituer une signature de groupe impliquée dans l'apprentissage social chez le diamant mandarin, ceux-ci ont soulevé plusieurs problèmes quant à la manière d'évaluer ces préférences sociales, lorsque plusieurs facteurs peuvent influencer la réponse de l'observateur. Pour identifier clairement des sources d'information fiables susceptibles d'influencer l'apprentissage social chez cette espèce modèle, les études futures devront être particulièrement prudentes quant au fait de contrôler tous les facteurs potentiellement confondants.

Conclusion

Ces différentes expériences ont permis de fournir une meilleure compréhension des aspects dynamiques de l'évolution culturelle des signaux de communication, un sujet d'importance majeure dans le domaine des sciences comportementales et des sciences du langage. Cette thèse possède de nombreux aspects pluridisciplinaires puisque l'étude du chant

des oiseaux est intéressante pour différents domaines tels que la linguistique (ex : transmission culturelle des caractéristiques vocales), la biologie évolutive (ex : fonctions des vocalisations et évolution de la culture vocale), les neurosciences (ex : bases neurales de la production vocale et de la perception) et la physique (ex : traitement du signal acoustique).

Appendix II:

Curriculum vitae

Lucille **LE MAGUER**

DOCTORANTE EN ÉTHOLOGIE

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Nanterre, France
11/12/1992
Permis B

FORMATION

2019 — **Doctorat en éthologie**
Université Paris Nanterre, France

2015 — **Master 2 en psychologie cognitive, parcours recherche** (MENTION: TRÈS BIEN)
Université Paris Nanterre, France

2014 — **Master 1 en éthologie** (MENTION: BIEN - RANG: 3/42)
Université Paris Nanterre, France

2013 — **Licence en biologie, parcours biologie des organismes** (RANG: 24/97)
Université Rennes 1, France

ACTIVITÉS DE RECHERCHE

2015-2019 (4 ans) — **Doctorante en éthologie**
Évolution culturelle du chant d'oiseau en laboratoire
Laboratoire Éthologie Cognition Développement, Nanterre, France

2014-2015 (7 mois) — **Stagiaire chargée de recherche**
Personnalité et apprentissage chez le Diamant Mandarin (Taeniopygia guttata)
Laboratoire Éthologie Cognition Développement, Nanterre, France

2014 (2 mois) — **Stagiaire chargée de recherche**
Mesure de la préférence des femelles pour le chant des mâles chez le Diamant Mandarin
Laboratoire Éthologie Cognition Développement, Nanterre, France

ENSEIGNEMENT

2018-2019	**96h**	Travaux dirigés de Neuroanatomie, 2e année de licence de Psychologie
	96h	Travaux dirigés de Biologie, 1e année de licence de Psychologie
2017-2018	**8h**	Travaux Pratiques de Psychobiologie comparée, 3e année de licence de Psychologie
	56h	Travaux dirigés de Biologie, 1e année de licence de Psychologie
2016-2017	**64h**	Travaux dirigés de Biologie, 1e année de licence de Psychologie
2014-2015	**24h**	Tutorat de Biologie en ligne, 1e année de licence de Psychologie

COMMUNICATIONS SCIENTIFIQUES

Communications orales

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Cultural evolution and artificial dialects in zebra finches (Taeniopygia guttata). European Conference on Behavioural Biology (ECBB), Liverpool, Angleterre. 9 au 12 aout 2018

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Apprentissage du chant et capacités cognitives chez le Diamant Mandarin (Taeniopygia guttata). Rencontre annuelle de la Société Française pour *l'Etude* du Comportement Animal (SFECA), Caen, France. 21 au 24 mars 2016

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Song learning and cognitive abilities in zebra finches (Taeniopygia guttata). Rencontre annuelle de *l'Université* Franco-Allemande (UFA), Nanterre, France. 10 et 11 décembre 2015

Geberzahn, N., **Le Maguer, L.,** Nagle, L., Zsebok, S., Aubin, T., Derégnaucourt, S. Towards an understanding of developmental and perceptual mechanisms of vocal individuality in the Zebra Finch (Taeniopygia guttata). XXV International Bioacoustics Congress (IBAC), Murnau, Allemagne. 6 au 12 septembre 2015

Geberzahn, N., **Le Maguer, L.,** Nagle, Aubin, T., Derégnaucourt, S. Transmission culturelle du chant, personnalité et capacités cognitives chez le Diamant Mandarin. Rencontre annuelle de la Société Française pour *l'Etude* du Comportement Animal (SFECA), Strasbourg, France. 21 au 23 avril 2015

Posters

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Artificial birdsong dialects in the lab: Song production learning in males and song preference in female zebra finches (Taeniopygia guttata). 1st International Student Course in Behavioural BiologyBehaviour, Villetaneuse, France. 20 au 21 septembre 2018.
- Prix poster -

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Artificial birdsong dialects in the lab: Song production learning in males and song preference in female zebra finches (Taeniopygia guttata). Behaviour, International Ethological Conference (IEC), Estoril, Portugal. 30 juillet au 4 août 2017

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Évolution culturelle du chant en laboratoire: apprentissage du chant et réseaux sociaux dans deux colonies de Diamants Mandarins (Taeniopygia guttata). Journée de la recherche de *l'Université* Paris Nanterre, Nanterre, France. 3 mars 2017

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Cultural evolution of birdsong in the lab: song learning and social networks in colonies of zebra finches (Taeniopygia guttata). Social Network Analysis Workshop (SNA Workshop), Radolfzell, Allemagne. 17 au 19 janvier 2017

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Song learning and cognitive abilities in zebra finches (Taeniopygia guttata). XXV International 8th European Conference on Behavioural Biology (ECBB), Vienne, Autriche. 12 au 15 juillet 2016

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Song learning and cognitive abilities in zebra finches (Taeniopygia guttata). Journée de la recherche de *l'Université* Paris Nanterre, Nanterre, France. 9 décembre 2015

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Song learning and cognitive abilities in zebra finches (Taeniopygia guttata). Journée de rassemblement du Groupement de Recherche en Ethologie (GDR) et de *l'Institut* Francilien *d'Ethologie* (IFE), Villetaneuse, France. 12 au 14 octobre 2015

Le Maguer, L., Geberzahn, N., Derégnaucourt, S. Song learning and cognitive abilities in zebra finches (Taeniopygia guttata). XXV International Bioacoustics Congress (IBAC), Murnau, Allemagne. 6 au 12 septembre 2015

EXPÉRIENCES PROFESSIONNELLES

2012→2014 (3 mois) **Stagiaire soigneuse**
Soins vétérinaires, manutention et remise en liberté d'animaux sauvages blessés

CEDAF, École vétérinaire de Maisons-Alfort, France

2011→2015 (7 mois) **Animatrice BAFA**
Animation pour jeunes enfants de 3 à 10 ans

Association ENJEU, Brissac-Quincé, France

2013-2014 (1 an) **Soutien scolaire et baby-sitting**
Garde et aide aux devoirs pour élèves de maternelle, primaire et collège

Agence La Bambinerie, Paris, France

LANGUES

Anglais	**Courant** (lu, écrit, parlé)
Italien	**Moyen** (lu, parlé)
Russe	**Faible** (lu)

INFORMATIQUE

Analyses statistiques	R – SigmaStat® – SigmaPlot®
Analyses acoustiques	Avisoft® – Sound Analysis Pro (SAP) – Sound Explorer – Goldwave – Songseq
Autres	Pack Microsoft Office® – Matlab®

AUTRES

Depuis 2016: Adhésion à la Société Française du Comportement Animal (SFECA)

Représentante des doctorants du laboratoire

Organisation d'un "Journal Club" au sein du laboratoire

Participation à l'émission TV E=M6 « Le langage des animaux »

Participation à un podcast pour le webzine Madmoizelle

Abstracts

RÉSUMÉ

Titre : Évolution culturelle du chant d'oiseau en laboratoire

Comme les humains, certains animaux non-humains présentent des schémas comportementaux considérés comme des cultures. Le chant des oiseaux, un comportement appris, constitue un bon modèle pour étudier l'évolution de la culture vocale. Le but de cette thèse est de suivre l'évolution culturelle du chant au sein de plusieurs colonies de diamants mandarins (*Taeniopygia guttata*), fondées par des mâles produisant un chant très similaire après avoir été entrainés avec le même modèle de chant. Deux colonies ont été fondées par des mâles chantant un même modèle de chant, et une colonie a été fondée par des mâles en chantant un autre. Dans ces conditions artificielles, le chant a évolué de telle sorte que la similarité au modèle initial a été maintenue dans le temps et que chaque modèle de chant a conduit à des spécificités acoustiques particulières. C'est la première preuve expérimentale que des dialectes de chant peuvent émerger chez le diamant mandarin, formant ainsi des cultures vocales distinctes. Chez cette espèce sociale, de telles variations au niveau du chant pourraient avoir un rôle biologique. C'est pourquoi leur implication dans la préférence des femelles et l'apprentissage social a été étudiée. Les femelles préfèrent le dialecte natif à un dialecte étranger. Pourtant, les individus des deux sexes ne sont pas plus susceptibles de copier le choix de nourriture d'un oiseau chantant le dialecte de leur propre colonie, que le choix d'un oiseau chantant un dialecte différent. Ce travail de thèse marque une étape dans l'étude de l'évolution culturelle du chant du diamant mandarin en laboratoire et contribue à une meilleure compréhension des aspects dynamiques de l'évolution culturelle des signaux de communication, un sujet d'importance majeure dans les sciences du langage.

Mots clés : évolution culturelle, chant d'oiseau, diamant mandarin, dialectes de chant, préférence des femelles, apprentissage social

ABSTRACT

Title: Cultural evolution of birdsong in the laboratory

For a long time, culture has been considered as a human specificity but there is extensive evidence in the animal kingdom that several species exhibit behavioural patterns considered as cultures. Birdsong is a learned behaviour and has been demonstrated as a valid model to study the evolution of vocal culture. The aim of this study is to track the cultural evolution of song in colonies of zebra finches (*Taeniopygia guttata*), starting with an extreme initial condition under which all male founders produce a very similar song after being trained with the same song model. Two colonies were founded by males singing a same song model and one colony was founded by males singing another song model. Overall, the results show that, in such artificial conditions, the song evolved in a way that the similarity to the initial model was maintained over time and each song model led to different acoustic specificities. This demonstration constitutes the first experimental evidence that song dialects can emerge in the zebra finch, forming distinct vocal cultures. Because such song variations could have biological significance in this social species, we investigated their implications for female preference and social learning. Female zebra finches preferred their native song dialect over a stranger one. Yet, birds of both sexes were not more likely to copy the food choice of a bird singing the dialect of their own colony than the choice of a bird singing a different dialect. This thesis work constitutes one step in understanding the cultural evolution of the zebra finch song in the laboratory and more generally, provides a better understanding of the dynamics of cultural evolution of communication signals, which represent an important topic in language research.

Keywords: cultural evolution, birdsong, zebra finch, song dialects, female preference, social learning