



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

Lucille Le Maguer, Sébastien Derégnaucourt, Nicole Geberzahn

## ► To cite this version:

Lucille Le Maguer, Sébastien Derégnaucourt, Nicole Geberzahn. Female preference for artificial song dialects in the zebra finch ( *Taeniopygia guttata* ). *Ethology*, 2021, 127 (7), pp.537-549. 10.1111/eth.13159 . hal-03350957

**HAL Id: hal-03350957**

**<https://hal.science/hal-03350957>**

Submitted on 21 Sep 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Le Maguer L, Derégnaucourt S, Geberzahn N. Female preference for artificial song dialects in the zebra finch (*Taeniopygia guttata*). *Ethology*. 2021;00:1– 13.

**Authors' pre-print**

**Editor's version available at the following:**

<https://doi.org/10.1111/eth.13159>

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

**Lucille Le Maguer<sup>1,2</sup>, Sébastien Derégnaucourt<sup>1,2,3,\*</sup> & Nicole Geberzahn<sup>1,2,\*</sup>**

<sup>1</sup> Laboratoire Éthologie Cognition Développement, Université Paris Nanterre, 200 Avenue de la République, F92001 Nanterre Cedex, France

<sup>2</sup> Université Paris Lumières, 140 rue du Chevaleret, 75013 Paris, France

<sup>3</sup> Institut Universitaire de France, 75005 Paris, France

Author's note

\* Joint authors.

Correspondence: lucille.lemaguer@gmail.com

## 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 artificially create different colony-wide song dialects. In this species, song plays a crucial role in mate choice and the importance of both subadult and adult song experience in shaping 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 songs similar to their colony's song. 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 also of a social preference. We discuss the potential role of song dialects in the context of social learning.

Keywords: female choice, birdsong, operant test, geographical variations, sexual preference, social preference

## Introduction

Geographical variation in phenotypic traits can have a central role in speciation processes, in particular if such traits play a role in mate choice (Edwards, Kingan, Calkins, Balakrishnan, Jennings, Swanson, & Sorenson, 2005; Miller, 1956). Birdsong is an example of such a trait as in many songbird species, geographical song variations have been reported, and mate attraction and stimulation is one of its main functions (Catchpole & Slater, 2008; Kroodsma, 2004; Podos & Warren, 2007). In such 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 (Marler & Tamura, 1962; Podos & Warren, 2007). Such vocal geographical variations can lead to song dialects and can be maintained over very long periods of time (Derryberry, 2007; García, Arrieta, Kopuchian, & Tubaro, 2015; Harbison, Nelson, & Hahn, 1999; Marler & Tamura, 1962; Trainer, 1983). Several hypotheses about the functions of dialects have been proposed (Catchpole & Slater, 2008). According to the "genetic adaptation hypothesis", geographical variation of birdsong allows 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). Geographical 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, West, & Eastzer, 1980; MacDougall-Shackleton, MacDougall-Shackleton, & Hahn, 2001; O'Loughlen & 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, Campbell, & Nordby, 2000; Payne, 1982, 1983). Song dialects may also play

an important role in group cohesion as they may signal group identity (Briefer, Aubin, Lehongre, & Rybak, 2008; Hausberger, Bigot, & Clergeau, 2008). 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 (Catchpole & Slater, 2008, but see Odom, Hall, Riebel, Omland, & Langmore, 2014). 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, memorising and reproducing the song of conspecifics, mainly adults (Derégnaucourt, 2011 but see Derégnaucourt & Gahr, 2013). 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, vocal changes are rarely observed (Immelmann, 1969). In the zebra finch, song plays a crucial role in mate choice and the link between song and female preference is well 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 his 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 show consistent preferences as adults (Lauay, Gerlach, Adkins-Regan, & DeVoogd, 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, female mate choice is based on different signal modalities, but it has been demonstrated that the song could potentially provide sufficient information about a 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

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

77       Until now, studies focusing on zebra finches suggested that dialects could not emerge  
78 in this species. Only weak geographical song variations have been found in different Australian  
79 populations (Zann, 1993) and it has been concluded that dispersal to and from colonies  
80 prevented the formation of colony-specific versions of the song (Zann, 1993). In domesticated  
81 populations of zebra finches, a high rate of learning errors probably prevents the establishment  
82 of song dialects (Lachlan, van Heijningen, ter Haar, & ten Cate, 2016). However, in our  
83 laboratory, we succeeded to create artificial song dialects. We did so by training male founders  
84 of three different colonies to produce a very good imitation of a song model (Le Maguer,  
85 Geberzahn, Nagle & Derégnaucourt, under review). Male offspring raised in these colonies  
86 developed songs with a high conformity to the song model, and each song model led to a  
87 different dialect (Derégnaucourt, Nagle, Gahr, Aubin, & Geberzahn, 2014; Le Maguer et al.,  
88 under review). Female offspring raised in those colonies heard different versions of a unique  
89 song type during their early life: the song dialect of their colony. These conditions allowed us  
90 to test for a link between song dialects and female preference in a widely studied species. Given  
91 that female zebra finches prefer songs they heard when they were young, we predicted that in  
92 each colony, females would prefer songs that resemble those produced by males of their colony.

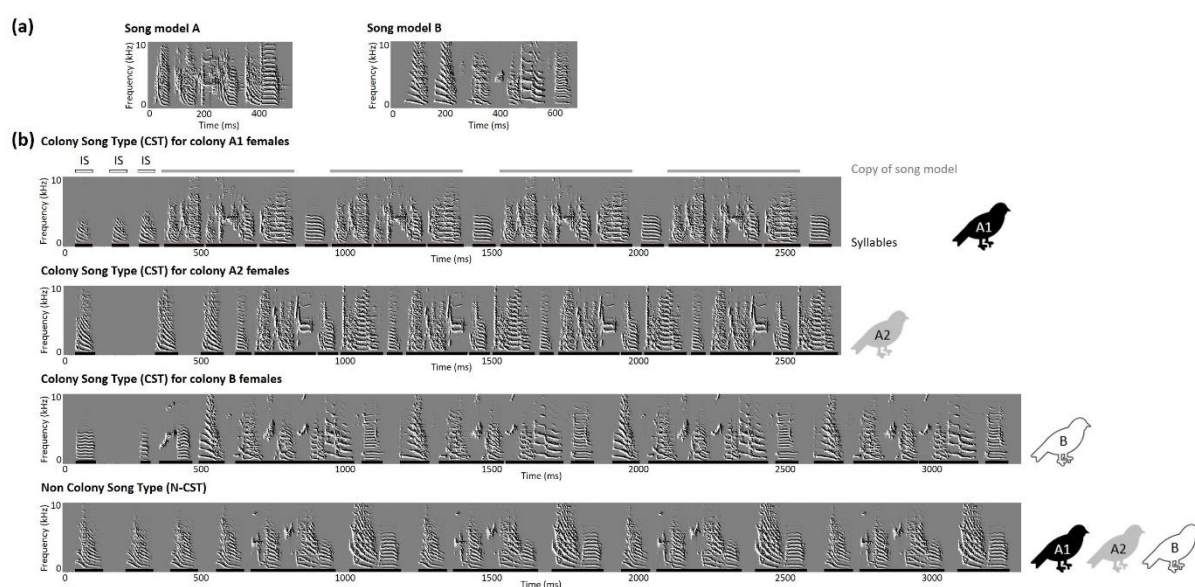
93       To verify this prediction, we tested female zebra finches with an operant conditioning  
94 paradigm (Riebel, 2000; Riebel & Slater, 1998; Riebel, Smallegange, Terpstra, & Bolhuis,

2002; Salvin, Derégnaucourt, Leboucher, & Amy, 2018). During the test, a female had the choice between two response keys, each triggering a different song type when pecked: 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 type that was different from the song type of her colony, which we refer to as the “Non-Colony Song Type” (N-CST). According to our hypothesis, we expected that females would peck more often on the response key triggering the CST than on the key triggering the N-CST.

## Materials and Methods

### Subjects and rearing conditions

All subjects in this experiment were adult female zebra finches that hatched and were raised in our laboratory. Subjects originated from three different colonies, each of them founded by males previously trained to produce the same song model (Le Maguer et al., under review). Two colonies (colony A1 and colony A2) were founded by males singing song model A (Figure 1a). The third colony (colony B) was founded by males singing a different song model, song model B (Figure 1a).





**Figure 1.** Spectrograms illustrating song models of colonies and of songs used as stimuli for the preference test. (a) Spectrograms of song model A and B that had been used to artificially create song dialects. Song model A and B consisted of a single motif each. (b) Example of one set of song stimuli (set #3) used in the female preference test of the present study. A set was composed of four different song stimuli. Each stimulus consisted of a bout in which the motif was repeated four times. Note that each female subject was exposed to only two out of four song stimuli of a given set: one Non-Colony Song Type (N-CST) and one Colony Song Type (CST), whereby both stimuli were produced by a male unfamiliar to her. Females from different colonies that were tested with the same set of song stimuli were exposed to a different CST stimulus according to their colony. In the first spectrogram (CST for colony A1 females), the different units of a typical zebra finch song are indicated. Introductory syllables (IS) are overlined in white. Syllables are underlined in black. Copies of the song model are overlined in grey. Bird silhouettes to the right of the spectrograms illustrate the females for whom such song stimuli were used: black silhouettes represent song stimuli for a colony A1 female, grey silhouettes represent song stimuli for a colony A2 female and white silhouettes represent song stimuli for a colony B female.

The number of colonies and choice of song models are inherent to the protocol of a previous study focusing on cultural evolution of birdsong (Le Maguer et al., under review). Briefly, after creating colony A1, we created a second colony using the same song model (song model A) but a smaller number of founders in order to test whether the number of founder males has an influence on the findings. We created the third colony using founder males singing a different song model in order to test whether results obtained for song model A could be generalised to another song type.

Details of how we set up colonies have been described elsewhere (Le Maguer et al. under review). Briefly, founder males and founder females of each colony were housed together in a communal aviary containing nest boxes and nesting material, so that they could reproduce freely until we obtained at least 34 male pupils per colony. In colony A1, we obtained a total of 48 male and 27 female offspring after 346 days. In colony A2 we obtained 34 male and 26

female offspring after 399 days. In colony B we obtained 35 male and 37 female offspring after 555 days. Birds were individually marked with three coloured rings one of which was always red and numbered. 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 those produced by the males of their own colony. All aviaries were set to a 14:10 light:dark (LD) schedule (lights on at 8 am - off at 10 pm) 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.

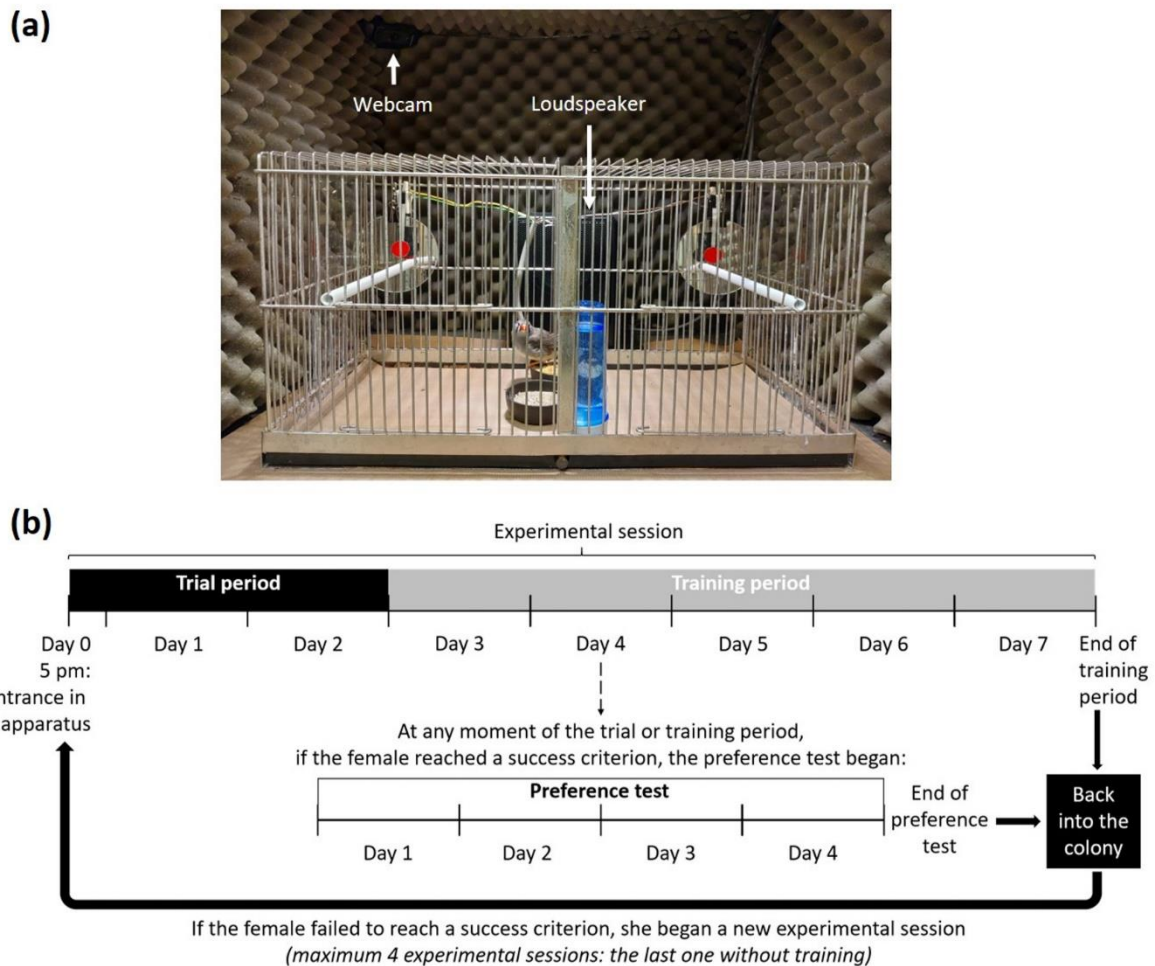
We tested a total of 63 females: 11 from colony A1, 21 from colony A2 and 31 from colony B. Females from colony A1 were tested at the age of  $1601 \pm 86$  days post-hatch (dph), females of colony A2 at  $792 \pm 106$  dph and females of colony B at  $655 \pm 89$  dph.

## Apparatus

We tested the preference of females for the dialect of their colony by using an operant task with song as a reward (Riebel, 2000; Riebel & Slater, 1998; Riebel et al., 2002; Salvin et al., 2018). The experimental 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). The apparatus consisted of a sound-proof chamber (85 x 65 x 60 cm) containing a metal cage (46 x 22 x 26 cm) with 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. Seeds, egg food, water and sand were available *ad libitum* throughout the experiment. When pecked, each red key triggered the playback of a song, broadcasted via a loudspeaker (Yamaha MS101 III, Frequency Response: 30 Hz - 20 kHz) located in between the two response keys. Songs were broadcast 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 sound-proof chamber was equipped with fans providing a low airflow 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, Lints, Derégnaucourt, Cimenser, & Mitra, 2004), this software controlled the playback and automatically switched songs between the two keys each night, to control for possible side preferences. The software kept track of all key 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. 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-proof chamber was equipped with a Logitech C920 webcam. 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. Females were housed with members of their colonies until being transferred to soundproof chambers for the experimental session.

## Stimuli

It has been demonstrated that female zebra finches are able to generalise their learnt preference for a specific song type (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 (CST and N-CST) were produced by unfamiliar birds. In a previous study we had conducted a detailed song analysis that revealed high similarities between males of colony A1 and colony A2 in song features such as syllable and element repertoire, song variability, inter-syllabic gap distribution

and song bout structure. At the same time, males from the colonies A1 and A2 differed from those of colony B with respect to these song features (Le Maguer et al., under review). Thus, we had created two different dialects: males from colony A1 and A2 sung one and the same song dialect, males of colony B sung another dialect. The CST for A1 females were songs produced by males of colony A2 and vice versa. Given the large number of males in these colonies, a large pool of songs was available to create the song stimuli. In contrast, no such second colony was available for females of colony B. Therefore, the CST for females of colony B were songs of different males that had been trained to produce an 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 Max Planck Institute for Ornithology in Seewiesen (Germany). Spectrographic illustrations of different stimuli that were used as a N-CST are presented in Figure S1.

### ***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 of directed songs. Recordings of directed songs are often polluted by cage noises due to courtship displays of males and calls produced by females. 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 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 and set the peak amplitude to 90% to all the sound files of each male, using Goldwave software (v6.36).

### ***Selection of songs based on the song model***

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). To select song stimuli that best represented the colony's song type, we chose songs from males that produced a very good copy of the song model. To do so, we quantified a similarity score between the copy of the male and the song model of his colony, using the song similarity procedure of SAP 2011 (Tchernichovski et al., 2000; Le Maguer et al., under review). Males whose songs were chosen as CST stimuli had a high similarity to the song model (mean  $\pm$  SD =  $87 \pm 8$ ).

### *Creation of song stimuli*

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 kept the natural gap durations between song motifs. To standardize all song stimuli, amplitude was root-mean square equalised with Praat software (peak digitally scaled to 0.99).

To minimise pseudoreplication, we created 10 unique sets of song stimuli, each set being composed of four songs produced by four different males: 1) one male producing a N-CST (conspecific song), 2) one male producing a CST for colony A1 females, 3) one male producing a CST for colony A2 females, 4) one male producing a CST for colony B females (Figure 1b). Note that out of those four stimuli, each female was exposed to only two stimuli during the operant test (one CST and one N-CST). Among the **10** sets, only seven contained a CST for females of colony B, as we did not have more unfamiliar males singing a good copy of the song

model B. Therefore, in colony A1 and A2, we assigned one out of 10 sets to each female, whereas in colony B, we assigned one out of **seven** sets to each female. The same N-CST was broadcasted to females from different colonies who were assigned the same set. However, the CST depended on the colony of the female and was thus different for females from different colonies (Table S1). Within one set, we matched song duration as much as possible (Table S1). The mean duration of songs ( $\pm$  SD) was: N-CST songs =  $4.09 \pm 1.10$  s; CST songs for females of colony A1 =  $3.75 \pm 0.99$  s; CST songs for females of colony A2 =  $3.73 \pm 1.14$  s; CST songs for females of colony B =  $3.37 \pm 0.47$  s. Within each colony, several females were tested with the same set (Table S2).

#### Preference test

Each female subject was taken from her colony and transferred to the apparatus at around 5 pm (day 0 of the experiment). From this moment on, the female had access to 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 learned the task if we detected at least 10 pecks on each key in one day (first learning criterion). The day on which this success criterion was reached was considered day 1 of the preference test. Following day 1 of the preference test, females had access to the keys during the three following days (day 2, 3 and 4 of the preference test), before transferring her back to her colony. Thus, the preference test lasted four full days and assignment of stimuli to response keys was reversed each night, in order to control for side preferences: on two days the CST was triggered by the right key, and

on two days the CST was 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 track of the pecks realised by females after each reinforcement session. If a 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 (i.e. the key on which they pecked more often) and reinforcing the non-preferred key during the training period. We assumed that with the preferred key covered, females would start to peck the non-preferred key and would continue to do so even after uncovering the previously preferred key. However, this was not the case. In Figure S2, we present a comparison of song preferences to side preferences at the colony level. For females exhibiting a side preference, 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 having spent at least a week 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 on, the test continued until day 4. Some females did not learn to press the keys during the



first three experimental sessions. Those females were transferred to the apparatus for a fourth experimental session, this time without any training. If a female still had not reached one of the two learning criteria at the end of this fourth experimental session, we considered that she failed the experiment. The procedure of the whole experiment is presented in Figure 2b. At any moment of the experiment, we could check whether a female pecked the keys on purpose using webcams that were running continuously during the day.

#### Notes on animal studies

All procedures reported here 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).

The following statements on sampling biases are made with reference to the STRANGE framework (Webster & Rutz, 2020). Social background: all females were raised in free range aviaries in which they could interact freely with all members of their colony (males and females) throughout their lives; Trappability and self-selection: all the females within the three colonies were tested, removing any possible bias due to trappability and self-selection; Rearing history: all tested females came from colonies that were created and reared in the same way, with access to the same resources and enrichment (see “Subjects and rearing conditions” section above); Acclimation and habituation: details concerning acclimation and habituation to the experimental set-up have been described above in the “Preference test” section; Natural changes in responsiveness: potential changes in females’ responsiveness in our experiment could be related to differences in their reproductive state. As zebra finches are considered opportunistic breeders and lack seasonality in breeding (Immelmann, 1968; Zann, 1996), we could not assess females' sexual receptivity before testing; Genetic make-up: all birds came from the same genetic background, as mentioned in the “Subject and rearing conditions” section; Experience: all females of this study had already been captured, handled and tested in sound-proof chambers

in other experiments previous to this study. As mentioned in the “Preference test” section, a training procedure has been done to adjust the experimental protocol to suit non- or slowly-engaging individuals. According to our above statements, we estimate the STRANGEness of our sample as low. All potential biases related to STRANGE framework that could be due to females’ experiences are discussed in the “Discussion” section.

## 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 when being 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.

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. We also calculated preference strength as the number of pecks for the preferred song type, divided by the number of pecks for the less preferred song type.

## 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 colony 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. We corrected p-values for multiplicity using the false discovery rate correction. To check whether a link existed between motivation and preference strength, we used Spearman's correlations because data were not normally distributed.

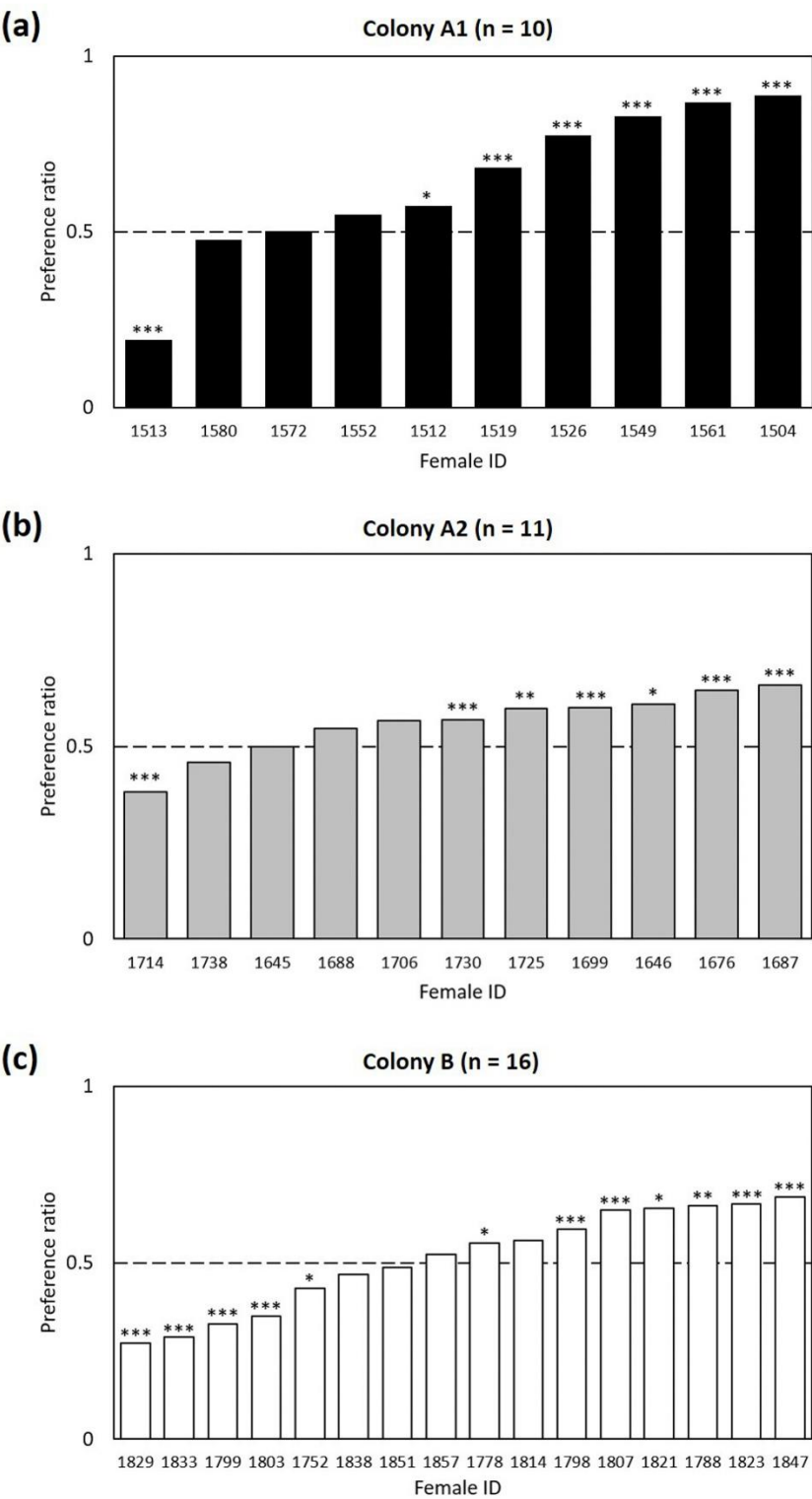
Finally, we tested whether the behavioural responses during the preference test differed between the three colonies to check whether there was a higher preference ratio for the CST or a higher number of pecks during the test in one of the three colonies. We ran two separate generalized mixed models (GLMMs), one for each of the 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 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 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup> or 4<sup>th</sup> experimental session) as a fixed effect. This variable is later referred to as "sessions to success". Both models included the number (ID) of the set of song stimuli the female was tested with, as a random effect. Due to high collinearity between the variables "female age" and "colony" we could not include female age in the model. Thus, we kept only the variables "colony" and "sessions to success" (there was no collinearity between these two variables). We used error distributions from the quasi family as we detected overdispersion in both models. 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 *emmeans* package in R (Lenth, 2018).

## Results

41 out of 63 tested females reached one of the two learning criteria. Four females pecked the keys less than 20 times on the second day of test. Those four females were thus excluded from the analysis. Therefore, the results for 37 females were used for further analysis (colony A1:  $n = 10$ ; colony A2:  $n = 11$ ; colony B:  $n = 16$ ). 15 out of these 37 females passed the preference test during the first experimental session (colony A1:  $n = 3$ ; colony A2:  $n = 5$ ; colony B:  $n = 7$ ), three during the second experimental session (colony A2:  $n = 1$ ; colony B:  $n = 2$ ), four during the third experimental session (colony A1:  $n = 3$ ; colony B:  $n = 1$ ), and 15 during the fourth experimental session (colony A1:  $n = 4$ ; colony A2:  $n = 5$ ; colony B:  $n = 6$ ) (Table S3). For the number of successful females tested with each set of song stimuli, see Table S2. Among the 37 females kept for analysis, some did not reach the first learning criterion due to their preference for one particular key over the other – i.e. they pecked the non-preferred key less often than 10 times a day (mean number of pecks per day  $\pm$  SD =  $1 \pm 2$ ). However, they did reach the second learning criterion. This side preference concerned 17 females: six in colony A1, three in colony A2 and eight in colony B. In the preference analysis of these females, we only focused on pecks on the preferred key and tested whether they pecked more often on the preferred key when it was triggering the CST or when it was triggering the N-CST.

After calculation of each female's preference ratio (number of pecks for the CST/total number of pecks), we witnessed that 26 out of the 37 females significantly preferred one of the two song types, i.e. their preference ratio was significantly different from 0.5 (Figure 3). This means they expressed a significant preference for one of the two song types that could be either the CST or the N-CST (colony A1: 7 out of 10, colony A2: 7 out of 11, colony B: 12 out of 16; Figure 3, Table 1 & Table S3). Additionally, among those 26 females out of 37 that showed a preference, 19 preferred the CST over the N-CST (six in colony A1 and A2, seven in colony B;

388 Figure 3, Table 1 & Table S3) and only seven preferred the N-CST over the CST (one in colony  
 389 A1 and A2, five in colony B; Figure 3, Table 1 & Table S3).



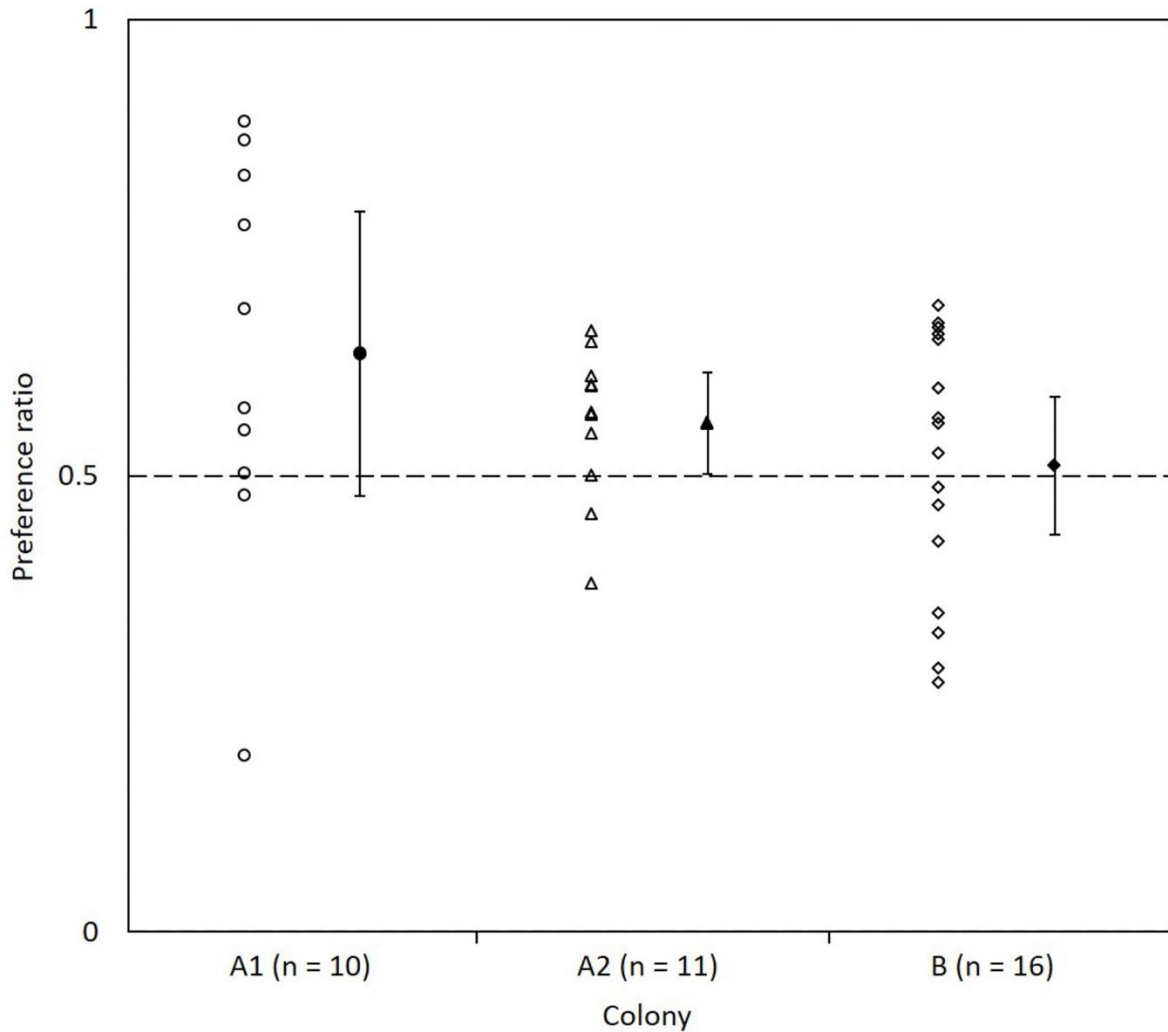
390  
 391 **Figure 3.** Preference ratios (pecks for the Colony Song Type (CST)/total number of pecks) for  
 392 each female of: (a) colony A1, (b) colony A2, and (c) colony B. Preference ratios approaching

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 and 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 without a preference	Females with a preference		
				For the CST	For the N-CST	Total
A1	10	<i>n</i>	3	6	1	7
		%	30	60	10	70
A2	11	<i>n</i>	4	6	1	7
		%	36	55	9	64
B	16	<i>n</i>	4	7	5	12
		%	25	44	31	75

However, this preference for the colony song type was not reflected at the colony level. 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). However, this significant difference disappeared when correcting for multiple testing ( $p_{adjusted} = 0.126$ ). In colony A1 and B, the mean preference ratio was not significantly different from chance level of 0.5 (colony A1:  $t = 1.94$ ,  $df = 9$ ,  $p = 0.084$ ,  $p_{adjusted} = 0.126$ ; colony B:  $t = 0.31$ ,  $df = 15$ ,  $p = 0.762$ ,  $p_{adjusted} = 0.762$ ; Figure 4).



**Figure 4.** Preference ratio for the Colony Song Type (CST) over the Non-Colony Song Type (N-CST) in each colony. Open symbols represent preference ratios of individual females. 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,  $p = 0.044$ ). This significant difference disappeared when correcting for multiple testing ( $p_{adjusted} = 0.126$ ).

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 often also had stronger preferences. However, there was no significant correlation between the total number of key pecks and preference strength in any of the colonies (colony A1:  $r_s = 0.139$ ,  $p = 0.707$ ; colony A2:  $r_s = -0.073$ ,  $p = 0.839$ ; colony B:  $r_s = 0.444$ ,  $p = 0.087$ ).

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 was higher in colony A1 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 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 *ns*, see Table 2). Two colonies differed in their activity levels: we found that females of colony A1 pecked significantly more often on 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 *ns*, see Table 2).



Table 2. Tukey post-hoc pairwise comparisons for 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	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Colony	A1 - A2	0.462	0.301	1.534	0.295	1.032	0.518	1.993	0.138
	A1 - B	<b>0.657</b>	<b>0.239</b>	<b>2.753</b>	<b>0.03</b>	<b>1.423</b>	<b>0.528</b>	<b>2.693</b>	<b>0.034</b>
	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

442

## 443 Discussion

444 In this study, many female zebra finches (19 out of 37) exhibited a clear preference for  
 445 the Colony Song Type (CST) over the Non-Colony Song Type (N-CST) whereas few females  
 446 (seven out of 37) exhibited a preference for the N-CST. Yet, this preference for songs that  
 447 resembled those produced by males of their colony was not reflected at the colony level.  
 448 Additionally, these individual preferences were not related to the level of motivation of the  
 449 females. The preference for the CST as well as the activity levels of females appeared to be  
 450 stronger in colony A1 than in the colony B, but both were not affected by the number of  
 451 experimental sessions females needed to reach either of the two learning criteria (10 pecks on  
 452 each key, or 20 pecks on one of the two keys on a same day).

Our results are consistent 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 many 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 songster. This confirms the females' ability to generalise the learnt song preference to songs of unfamiliar males, an ability already demonstrated for zebra finches (Clayton, 1990; Riebel, 2009).

Even if some weak geographical variations in the song had been described in Australian populations of zebra finches (Zann, 1993), the salience of these variations to females have not been studied so far. Based on artificially created dialects of laboratory colonies, we were able to show here that these acoustic variations matter to female zebra finches. The significance of local song dialects to females for mate choice decisions has been investigated in other species exhibiting geographical song variations naturally. For example, female Nuttall's white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) were more stimulated by male song of their natal dialect than by male song of adjacent dialects (Baker, 1983). According to the "genetic adaptation hypothesis" we propose that song dialects might matter to female zebra finches in the context of mate choice, as a cue for assortative mating (Tomback & Baker, 1984). In other words, pairing with a male singing the local song type would ensure the female that her offspring will be genetically adapted to the local environment and will have a better survival and reproductive success than foreign birds (Marler & Tamura, 1962, 1964; Nottebohm, 1969, 1972; Payne, 1981). Furthermore, it has been argued that female preferences play an important

role in the stability of song dialects (reviews in Baker & Cunningham, 1985; Payne, 1981; 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 could influence the stability of dialects (O’Loghlen & Rothstein, 1995, 2003). The brown-headed cowbird is an interesting case as it is a brood parasitic species in which young birds are not exposed to conspecific song during their early life. Several studies in the zebra finch proposed that male song learning may likewise be influenced by females. For instance, young males imitate a tutor song better when housed with a hearing female than when housed without a female (Adret, 2004) and worse when housed with a deaf female than when housed with a hearing 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). Given that in the current study females mostly preferred songs of their home dialect, female preferences might have played a role in the establishment and stability of artificial song dialects in our colonies of zebra finches. That is, females’ preferences for the CST might have guided young males to conform to this song model.

In most female preference studies on zebra finches, female subjects were sexually naive and housed in single-sex groups with no contact of any sort with males prior to the preference test (e.g. Holveck & Riebel, 2007; Riebel, 2000; Riebel et al., 2002). In contrast, females in the current study spent their whole lives with males with whom they could interact freely and reproduce during the course of the communal breeding. Their exhibited preferences might therefore have been weaker than if they had been housed separately from males. Mated female zebra finches express a significant preference for their mate's song over an unfamiliar one (Miller, 1979b). Females who did not show a clear preference for the CST in the current study might have been paired to males producing a poor version of this song type. In fact, even if

most males conformed to the colony's song type, some males produced songs that deviated from it (Derégnaucourt et al., 2014; Le Maguer et al., under review). It is possible that some of our females were paired to males producing such deviant versions of the colony song type, a possibility that we were not able to verify as we did not keep track of their pair bonds.

Despite the individual preferences of females for the CST, this preference was not reflected at the colony level. 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 song features. It rather seems that experience-dependent song preferences of a female zebra finch might interplay with song features of the male's song (such as syllable diversity and spectro-temporal details) to determine which song that female finds attractive (Riebel, 2009). Nevertheless, we cannot exclude that some females in the current study preferred certain N-CST stimuli because of particular sound characteristics.

One could have expected an effect of the number of experimental sessions needed to reach either of the two learning criteria on the preference strength 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. This is probably not due to the nature of the song dialect (A or B), as females of colony A2 and B did not differ in those variables. It has been reported that experiences of females during adulthood could influence their song preferences (e.g. in canaries, Béguin, Leboucher, & Kreutzer, 1998; Nagle & Kreutzer, 1997). In zebra finches, females can develop preferences as adults (Clayton,

1988; Miller, 1979b; Riebel, 2009). Thus, we could assume that our females' adult experiences 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.

In zebra finches, the lack of seasonality in breeding (Immelmann, 1968; Zann, 1996) raises some issues concerning the nature of the observed preferences in females. In our study we did not test for female sexual receptivity. Therefore, we wonder whether females that showed a preference for the CST expressed 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 the future. In zebra finches, the classical observer-demonstrator paradigm has been proven effective to assess social learning in a context of food choice (Benskin, Mann, Lachlan, & Slater, 2002; Guillette & Healy, 2014; Katz & Lachlan, 2003; Riebel, Spierings, Holveck, & Verhulst, 2012). Therefore, if song dialects do constitute a social marker, an observer might 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 could 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 investigate whether song dialects can be used as an affiliative signal in the context of social learning in this model species.

## Acknowledgements

This work was supported by a grant from the French National Agency of Research (ANR-12-BSH2-0009) and the Institut Universitaire de France. LLM was supported by a PhD grant from the University Paris Nanterre. We thank Philippe Groué, Emmanuelle Martin and Ophélie Bouillet for taking care of the birds, Katarina Riebel for her valuable advices on the experimental design and creation of stimuli and Maxime Pineaux for help with statistics.

## 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. doi: 10.1007/s10164-003-0094-y
- 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. doi: 10.1007/BF00302898
- Baker, Myron Charles, & Cunningham, M. A. (1985). The Biology of Bird-Song Dialects. *Behavioral and Brain Sciences*, 8(1), 85-100. doi: 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. doi: 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. doi: 10.1163/156853998792913500

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

580 Benskin, C. M. H., Mann, N. I., Lachlan, R. F., & Slater, P. J. B. (2002). Social learning directs  
581 feeding preferences in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, 64(5),  
582 823-828. doi: 10.1006/anbe.2002.2005

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

586 Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews*, 78(4),  
587 575-595.

588 Carouso-Peck, S., & Goldstein, M. H. (2019). Female Social Feedback Reveals Non-imitative  
589 Mechanisms of Vocal Learning in Zebra Finches. *Current Biology*, (29), 631-636. doi:  
590 10.1016/j.cub.2018.12.026

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

593 Clayton, N. S. (1988). Song discrimination learning in zebra finches. *Animal Behaviour*, 36(4),  
594 1016-1024. doi: 10.1016/S0003-3472(88)80061-7

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

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

600 Derégnaucourt, S. (2011). Birdsong learning in the laboratory, with especial reference to the  
 601 song of the Zebra Finch (*Taeniopygia guttata*). *Interaction Studies*, 12(2), 324-350. doi:  
 602 10.1075/is.12.2.07der  
 603 Derégnaucourt, S., & Gahr, M. (2013). Horizontal transmission of the father's song in the zebra  
 604 finch (*Taeniopygia guttata*). *Biology Letters*, 9(4), 20130247. doi:  
 605 10.1098/rsbl.2013.0247  
 606 Derégnaucourt, S., Nagle, L., Gahr, M., Aubin, T., & Geberzahn, N. (2014). Cultural Evolution  
 607 of Birdsong in the Laboratory. *Neuroscience annual meeting 2014*.  
 608 Derryberry, E. P. (2007). Evolution of Bird Song Affects Signal Efficacy : An Experimental  
 609 Test Using Historical and Current Signals. *Evolution*, 61(8), 1938-1945. doi:  
 610 10.1111/j.1558-5646.2007.00154.x  
 611 Edwards, S. V., Kingan, S. B., Calkins, J. D., Balakrishnan, C. N., Jennings, W. B., Swanson,  
 612 W. J., & Sorenson, M. D. (2005). Speciation in birds : Genes, geography, and sexual  
 613 selection. *Proceedings of the National Academy of Sciences*, 102(suppl 1), 6550-6557.  
 614 doi: 10.1073/pnas.0501846102  
 615 García, N. C., Arrieta, R. S., Kopuchian, C., & Tubaro, P. L. (2015). Stability and change  
 616 through time in the dialects of a Neotropical songbird, the Rufous-collared Sparrow.  
 617 *Emu*, 115(4), 309-316.  
 618 Guillette, L. M., & Healy, S. D. (2014). Mechanisms of copying behaviour in zebra finches.  
 619 *Behavioural Processes*, 108, 177-182. doi: 10.1016/j.beproc.2014.10.011  
 620 Harbison, H., Nelson, D. A., & Hahn, T. P. (1999). Long-Term Persistence of Song Dialects in  
 621 the Mountain White-Crowned Sparrow. *The Condor*, 101(1), 133-148. doi:  
 622 10.2307/1370454  
 623 Hausberger, M., Bigot, E., & Clergeau, P. (2008). Dialect use in large assemblies : A study in  
 624 European starling *Sturnus vulgaris* roosts. *Journal of Avian Biology*, 39(6), 672-682.



625 Holveck, M. J., & Riebel, K. (2007). Preferred songs predict preferred males : Consistency and  
 626 repeatability of zebra finch females across three test contexts. *Animal Behaviour*, 74(2),  
 627 297-309.

628 Houx, A. B., & ten Cate, C. (1999). Song learning from playback in zebra finches : Is there an  
 629 effect of operant contingency? *Animal Behaviour*, 57(4), 837-845. doi:  
 630 10.1006/anbe.1998.1046

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

633 Immelmann, Klaus. (1968). Zur biologischen Bedeutung des Estrildidengesanges. *Journal für*  
 634 *Ornithologie*, 109(3), 284-299. doi: 10.1007/BF01678374

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

637 Katz, M., & Lachlan, R. F. (2003). Social learning of food types in zebra finches (*Taenopygia*  
 638 *guttata*) is directed by demonstrator sex and feeding activity. *Animal Cognition*, 6(1),  
 639 11-16. doi: 10.1007/s10071-003-0158-y

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

643 Kroodsma, D. E. (2004). The diversity and plasticity of birdsong. *Nature's music: the science*  
 644 *of birdsong*, 108-131.

645 Lachlan, R. F., van Heijningen, C. A., ter Haar, S. M., & ten Cate, C. (2016). Zebra Finch Song  
 646 Phonology and Syntactical Structure across Populations and Continents—A  
 647 Computational Comparison. *Frontiers in Psychology*, 7. Consulté à l'adresse  
 648 <http://www.ncbi.nlm.nih.gov/pmc/articles/PMC4935685/>

649 Lauay, C., Gerlach, N. M., Adkins-Regan, E., & DeVoogd, T. J. (2004). Female zebra finches  
 650 require early song exposure to prefer high-quality song as adults. *Animal Behaviour*,  
 651 68(6), 1249-1255. doi: 10.1016/j.anbehav.2003.12.025  
 652 Lenth, R. V. (2018). *Estimated Marginal Means, aka Least Squares Means. R Package version*  
 653 *1.1*.  
 654 MacDougall-Shackleton, E. A., & MacDougall-Shackleton, S. A. (2001). Cultural and Genetic  
 655 Evolution in Mountain White-Crowned Sparrows : Song Dialects Are Associated with  
 656 Population Structure. *Evolution*, 55(12), 2568-2575. doi: 10.1111/j.0014-  
 657 3820.2001.tb00769.x  
 658 MacDougall-Shackleton, S. A., MacDougall-Shackleton, E. A., & Hahn, T. P. (2001).  
 659 Physiological and behavioural responses of female mountain white-crowned sparrows  
 660 to natal-and foreign-dialect songs. *canadian Journal of Zoology*, 79(2), 325-333.  
 661 Marler, P., & Tamura, M. (1962). Song « Dialects » in Three Populations of White-Crowned  
 662 Sparrows. *The Condor*, 64(5), 368-377. doi: 10.2307/1365545  
 663 Marler, P., & Tamura, M. (1964). Culturally transmitted patterns of vocal behavior in sparrows.  
 664 *Science*, 146(3650), 1483-1486.  
 665 Miller, A. H. (1956). Ecologic Factors that Accelerate Formation of Races and Species of  
 666 Terrestrial Vertebrates. *Evolution*, 10(3), 262-277. JSTOR. doi: 10.2307/2406011  
 667 Miller, D. B. (1979a). Long-term recognition of father's song by female zebra finches. *Nature*,  
 668 280, 389-391.  
 669 Miller, D. B. (1979b). The acoustic basis of mate recognition by female zebra finches  
 670 (*Taeniopygia guttata*). *Animal Behaviour*, 27, 376-380.  
 671 Nagle, L., & Kreutzer, M. L. (1997). Adult female domesticated canaries can modify their song  
 672 preferences. *Canadian Journal of Zoology*, 75(8), 1346-1350. doi: 10.1139/z97-759

673 Nottebohm, F. (1969). The song of the chingolo, *Zonotrichia capensis*, in Argentina :  
 674 Description and evaluation of a system of dialects. *The Condor*, 71(3), 299-315.  
 675 Nottebohm, F. (1972). The Origins of Vocal Learning. *The American Naturalist*, 106(947),  
 676 116-140. doi: 10.1086/282756  
 677 Odom, K. J., Hall, M. L., Riebel, K., Omland, K. E., & Langmore, N. E. (2014). Female song  
 678 is widespread and ancestral in songbirds. *Nature Communications*, 5(1), 1-6. doi:  
 679 10.1038/ncomms4379  
 680 O’Loughlen, A. L., & Rothstein, S. I. (1995). Culturally correct song dialects are correlated with  
 681 male age and female song preferences in wild populations of brown-headed cowbirds.  
 682 *Behavioral Ecology and Sociobiology*, 36(4), 251-259. doi: 10.1007/BF00165834  
 683 O’Loughlen, A. L., & Rothstein, S. I. (2003). Female preference for the songs of older males and  
 684 the maintenance of dialects in brown-headed cowbirds (*Molothrus ater*). *Behavioral*  
 685 *Ecology and Sociobiology*, 53(2), 102-109. doi: 10.1007/s00265-002-0551-6  
 686 Payne, R. B. (1981). *Population structure and social behaviour: Models for testing the*  
 687 *ecological significance of song dialects in birds: In: Alexander RD & Tinkle DW (eds):*  
 688 *Natural selection and social behaviour: Recent Research and New Theory*. Chiron  
 689 Press. New York: 108.  
 690 Payne, R. B. (1982). Ecological Consequences of Song Matching: Breeding Success and  
 691 Intraspecific Song Mimicry in Indigo Buntings. *Ecology*, 63(2), 401-411. doi:  
 692 10.2307/1938958  
 693 Payne, R. B. (1983). The social context of song mimicry : Song-matching dialects in indigo  
 694 buntings (*Passerina cyanea*). *Animal Behaviour*, 31(3), 788-805. doi: 10.1016/S0003-  
 695 3472(83)80236-X

696 Podos, J., & Warren, P. S. (2007). The Evolution of Geographic Variation in Birdsong. In  
 697 *Advances in the Study of Behavior* (Vol. 37, p. 403-458). Academic Press. doi:  
 698 10.1016/S0065-3454(07)37009-5  
 699 Riebel, K. (2000). Early exposure leads to repeatable preferences for male song in female zebra  
 700 finches. *Proceedings of the Royal Society of London. Series B: Biological Sciences*,  
 701 267(1461), 2553-2558.  
 702 Riebel, K. (2003). The “Mute” Sex Revisited : Vocal Production and Perception Learning in  
 703 Female Songbirds. In *Advances in the Study of Behavior* (Vol. 33, p. 49-86). Academic  
 704 Press. doi: 10.1016/S0065-3454(03)33002-5  
 705 Riebel, K. (2009). Song and female mate choice in zebra finches : A review. *Advances in the*  
 706 *Study of Behavior*, 40, 197-238.  
 707 Riebel, K., & Slater, P. J. B. (1998). Testing female chaffinch song preferences by operant  
 708 conditioning. *Animal Behaviour*, 56(6), 1443-1453.  
 709 Riebel, K., & Smallegange, I. M. (2003). Does Zebra finch (*Taeniopygia guttata*) preference  
 710 for the (familiar) father’s song generalize to the songs of unfamiliar brothers? *Journal*  
 711 *of Comparative Psychology*, 117(1), 61-66. doi: 10.1037/0735-7036.117.1.61  
 712 Riebel, K., Smallegange, I. M., Terpstra, N. J., & Bolhuis, J. J. (2002). Sexual equality in zebra  
 713 finch song preference : Evidence for a dissociation between song recognition and  
 714 production learning. *Proceedings of the Royal Society of London. Series B: Biological*  
 715 *Sciences*, 269(1492), 729-733. doi: 10.1098/rspb.2001.1930  
 716 Riebel, K., Spierings, M. J., Holveck, M.-J., & Verhulst, S. (2012). Phenotypic plasticity of  
 717 avian social-learning strategies. *Animal Behaviour*, 84(6), 1533-1539. doi:  
 718 10.1016/j.anbehav.2012.09.029

719 Rothstein, S. I., & Fleischer, R. C. (1987). Vocal Dialects and Their Possible Relation to Honest  
720 Status Signalling in the Brown-Headed Cowbird. *The Condor*, 89(1), 1-23. doi:  
721 10.2307/1368756

722 Salvin, P., Derégnaucourt, S., Leboucher, G., & Amy, M. (2018). Consistency of female  
723 preference for male song in the domestic canary using two measures: Operant  
724 conditioning and vocal response. *Behavioural Processes*, 157, 238-243. doi:  
725 10.1016/j.beproc.2018.10.004

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

728 Tchernichovski, O., Lints, T. J., Derégnaucourt, S., Cimenser, A., & Mitra, P. P. (2004).  
729 Studying the Song Development Process: Rationale and Methods. *Annals of the New*  
730 *York Academy of Sciences*, 1016(1), 348-363. doi: 10.1196/annals.1298.031

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

734 Tomback, D. F., & Baker, M. C. (1984). Assortative mating by white-crowned sparrows at song  
735 dialect boundaries. *Animal Behaviour*, 32(2), 465-469. doi: 10.1016/S0003-  
736 3472(84)80282-1

737 Trainer, J. M. (1983). Changes in Song Dialect Distributions and Microgeographic Variation  
738 in Song of White-Crowned Sparrows (*Zonotrichia leucophrys nuttalli*). *The Auk*, 100(3),  
739 568-582. doi: 10.1093/auk/100.3.568

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

742 Webster, M. M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*,  
743 582(7812), 337-340. doi: 10.1038/d41586-020-01751-5

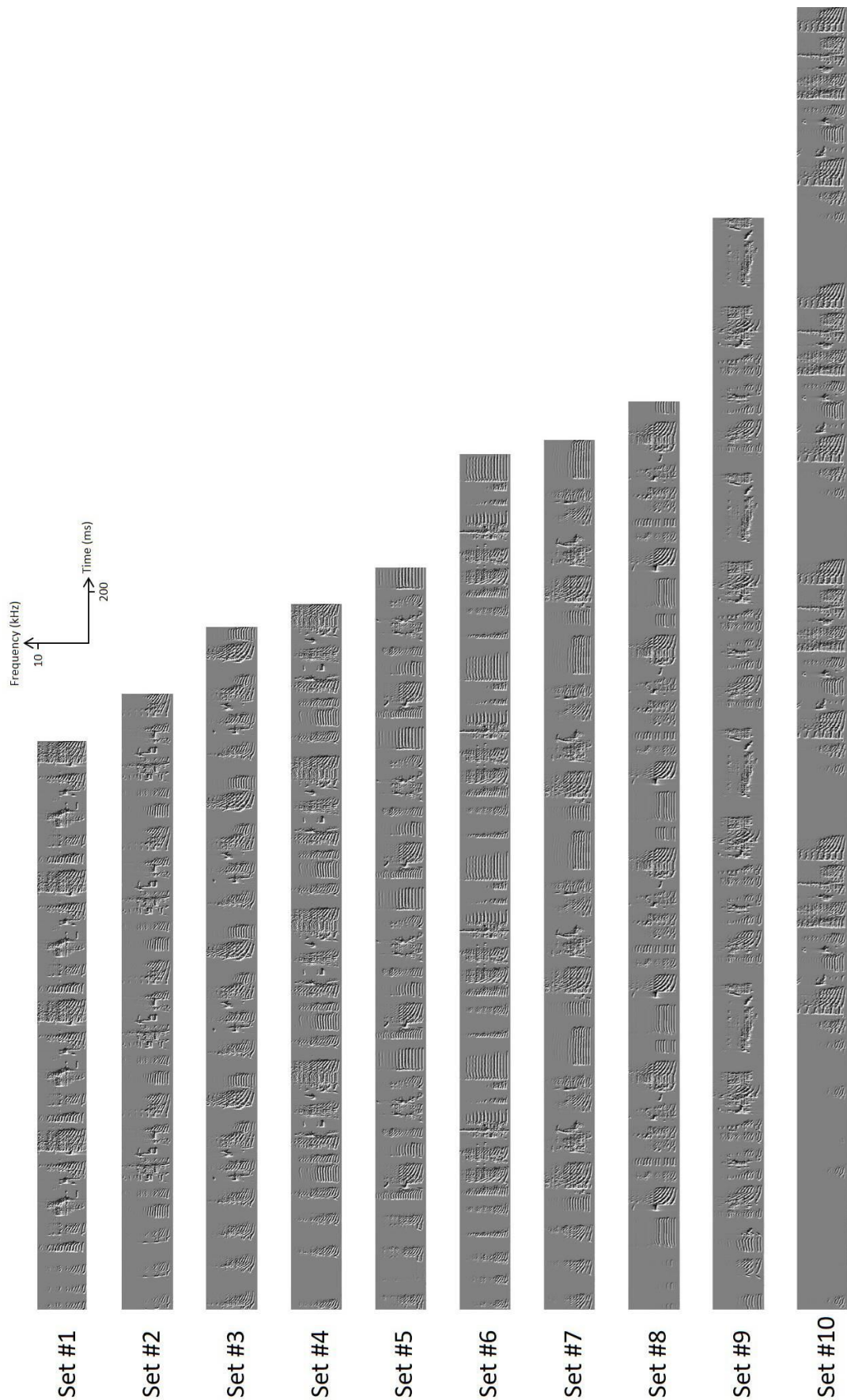
744 Widemo, F., & Saether, S. A. (1999). Beauty is in the eye of the beholder : Causes and  
 745 consequences of variation in mating preferences. *Trends in Ecology & Evolution*, 14(1),  
 746 26-31.

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

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

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

753



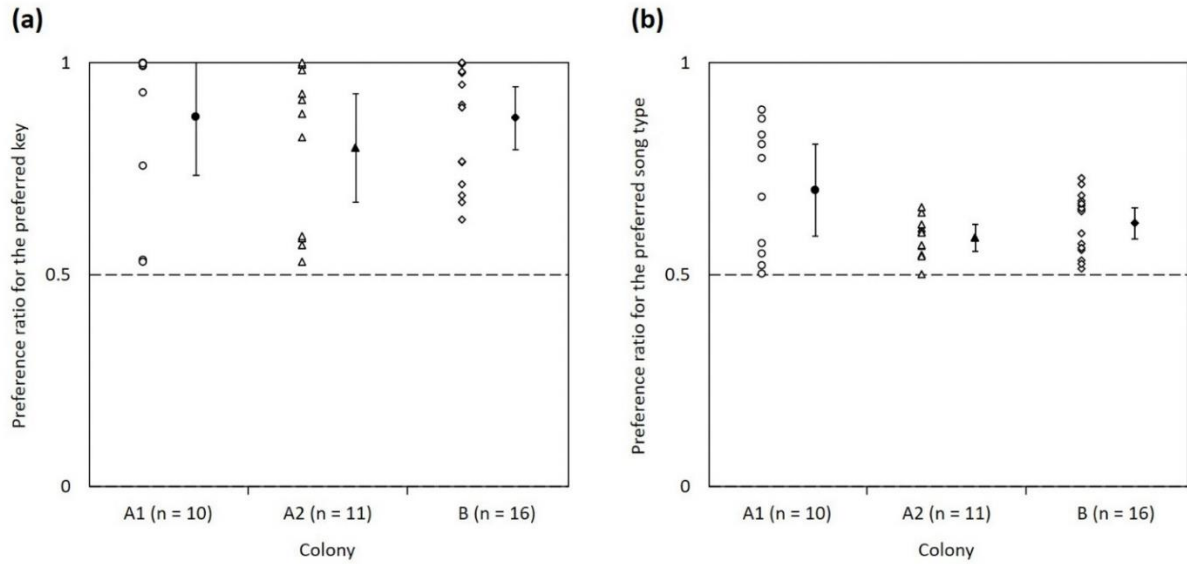
**Figure S1. Spectrograms of songs used as a Non-Colony Song Type (N-CST) stimulus.**

There was a different N-CST stimulus in each set of song stimuli (a 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 were recorded from 10 different adult males originating from the Max Planck Institute for Ornithology in Seewiesen (Germany).

**Comparison of song preference vs. side preference**

We compared song preferences to side preferences by calculating two additional preference ratios: 1) the preference ratio for the preferred key (either right or left): total number of pecks on the key on which a female pecked more often during the four days of test, divided by the grand total of pecks during the four days period; 2) the preference ratio for the preferred song type (independent of whether it was the CST or the N-CST): total number of pecks for the song type for which a female pecked more often during the four days of test, divided by the grand total of pecks during the four days period. To investigate whether there was a significant side preference and song preference at the colony level in each colony, we checked whether the mean preference ratios were greater than chance level by comparing it to 0.5 using one-sample t-tests. We corrected p-values for multiplicity using the false discovery rate correction. Even though the effect of song preference appears weaker than the effect of side preference (i.e. mean preference ratios are closer to the dashed line in panel (b) than in panel (a) of Figure S2), females still show a highly significant preference for one of the two song types.





**Figure S2. Comparison of side preferences and song preferences in each colony.** Open symbols represent individual females' preference ratios. Filled symbols represent the mean preference ratio (with 95% confidence interval). (a) Preference ratio for the preferred key over the non-preferred key. The mean preference ratio was significantly different from a 0.5 preference ratio (dashed line) in all colonies (colony A1:  $t = 6.06$ ,  $df = 9$ ,  $p < 0.001$ ,  $p_{adjusted} < 0.001$ ; colony A2:  $t = 5.2$ ,  $df = 10$ ,  $p < 0.001$ ,  $p_{adjusted} < 0.001$ ; colony B:  $t = 10.6$ ,  $df = 15$ ,  $p < 0.001$ ,  $p_{adjusted} < 0.001$ ). (b) Preference ratio for the preferred song type over the non-preferred song type. The mean preference ratio was significantly different from a 0.5 preference ratio (dashed line) in all colonies (colony A1:  $t = 4.16$ ,  $df = 9$ ,  $p = 0.0024$ ,  $p_{adjusted} = 0.0024$ ; colony A2:  $t = 6.09$ ,  $df = 10$ ,  $p < 0.001$ ,  $p_{adjusted} < 0.001$ ; colony B:  $t = 6.99$ ,  $df = 15$ ,  $p < 0.001$ ,  $p_{adjusted} < 0.001$ ).

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

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	-

795

796

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

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

798

799 *Note:* Tested females: females that entered the testing apparatus. Successful females: females

800 that reached one of the success criteria and completed the entire preference test.

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

802 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	<i>p</i> -value of binomial test
A1	1504	1	776	874	<b>0.89</b>	<b>&lt; 0.001</b>
	1512	3	195	340	<b>0.57</b>	<b>0.008</b>
	1513	4	56	291	<b>0.19</b>	<b>&lt; 0.001</b>
	1519	1	2055	3012	<b>0.68</b>	<b>&lt; 0.001</b>
	1526	4	2337	3020	<b>0.77</b>	<b>&lt; 0.001</b>
	1549	3	272	328	<b>0.83</b>	<b>&lt; 0.001</b>
	1552	4	206	375	0.55	0.063
	1561	3	998	1150	<b>0.87</b>	<b>&lt; 0.001</b>
	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	<b>0.61</b>	<b>0.006</b>
	1676	1	104	161	<b>0.65</b>	<b>&lt; 0.001</b>
	1687	4	108	164	<b>0.66</b>	<b>&lt; 0.001</b>
	1688	4	125	229	0.55	0.186
	1699	1	495	826	<b>0.60</b>	<b>&lt; 0.001</b>
	1706	4	241	425	0.57	0.59
	1714	1	144	377	<b>0.38</b>	<b>&lt; 0.001</b>
	1725	1	186	311	<b>0.60</b>	<b>&lt; 0.001</b>
	1730	2	2030	3566	<b>0.57</b>	<b>&lt; 0.001</b>
	1738	4	108	236	0.46	0.216
B	1752	3	153	358	<b>0.43</b>	<b>0.007</b>
	1778	1	244	438	<b>0.56</b>	<b>0.019</b>
	1788	4	53	80	<b>0.66</b>	<b>0.005</b>
	1798	4	1656	2779	<b>0.60</b>	<b>&lt; 0.001</b>
	1799	1	142	434	<b>0.33</b>	<b>&lt; 0.001</b>
	1803	1	84	241	<b>0.35</b>	<b>&lt; 0.001</b>
	1807	4	133	205	<b>0.65</b>	<b>&lt; 0.001</b>
	1814	1	72	128	0.56	0.185
	1821	1	38	58	<b>0.66</b>	<b>0.025</b>
	1823	4	174	261	<b>0.67</b>	<b>&lt; 0.001</b>
	1829	1	72	264	<b>0.27</b>	<b>&lt; 0.001</b>
	1833	4	147	510	<b>0.29</b>	<b>&lt; 0.001</b>
	1838	2	86	184	0.47	0.417
	1847	4	153	223	<b>0.69</b>	<b>&lt; 0.001</b>
	1851	1	106	218	0.49	0.735
	1857	2	186	355	0.52	0.396

803