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

Lucille Le Maguer^{1,2}, Sébastien Derégnaucourt^{1,2,3,*} & Nicole Geberzahn^{1,2,*}

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

² Université Paris Lumières, 140 rue du Chevaleret, 75013 Paris, France

³ Institut Universitaire de France, 75005 Paris, France

Author's note

* Joint authors.

Correspondence: lucille.lemaguer@gmail.com

1 **Abstract**

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

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

20 **Introduction**

21 Geographical variation in phenotypic traits can have a central role in speciation
22 processes, in particular if such traits play a role in mate choice (Edwards, Kingan, Calkins,
23 Balakrishnan, Jennings, Swanson, & Sorenson, 2005; Miller, 1956). Birdsong is an example of
24 such a trait as in many songbird species, geographical song variations have been reported, and
25 mate attraction and stimulation is one of its main functions (Catchpole & Slater, 2008;
26 Kroodsma, 2004; Podos & Warren, 2007). In such species, males of a same geographical
27 location sing the same song type or share a substantial part of their song repertoire whereas
28 males of different locations vary in their songs (Marler & Tamura, 1962; Podos & Warren,
29 2007). Such vocal geographical variations can lead to song dialects and can be maintained over
30 very long periods of time (Derryberry, 2007; García, Arrieta, Kopuchian, & Tubaro, 2015;
31 Harbison, Nelson, & Hahn, 1999; Marler & Tamura, 1962; Trainer, 1983). Several hypotheses
32 about the functions of dialects have been proposed (Catchpole & Slater, 2008). According to
33 the "genetic adaptation hypothesis", geographical variation of birdsong allows individuals to
34 recognize and mate with individuals of the same population, promoting the maintenance and
35 development of local adaptations (MacDougall-Shackleton & MacDougall-Shackleton, 2001;
36 Marler & Tamura, 1962, 1964; Nottebohm, 1969, 1972). Geographical variation in song could
37 thus influence female mating preferences (Catchpole & Slater, 2008; Searcy & Yasukawa,
38 1996), with females preferring males singing their natal or local song dialect (King, West, &
39 Eastzer, 1980; MacDougall-Shackleton, MacDougall-Shackleton, & Hahn, 2001; O'Loughlen &
40 Rothstein, 1995; Searcy & Andersson, 1986). According to the "social adaptation hypothesis",
41 song dialects affect social and sexual interactions, but dialectal populations should not be
42 genetically isolated from each other (Payne, 1981). Some studies show indeed a positive
43 correlation between vocal sharing and the maintenance of a territory and/or the reproductive
44 success (Beecher, Campbell, & Nordby, 2000; Payne, 1982, 1983). Song dialects may also play

45 an important role in group cohesion as they may signal group identity (Briefer, Aubin,
46 Lehongre, & Rybak, 2008; Hausberger, Bigot, & Clergeau, 2008). It has been shown that song
47 could increase social cohesion in highly social species, such as the European starling (*Sturnus*
48 *vulgaris*; Hausberger et al., 2008).

49 Singing behaviour is often sexually dimorphic, as many sexually selected traits
50 (Catchpole & Slater, 2008, but see Odom, Hall, Riebel, Omland, & Langmore, 2014). This is
51 the case in the zebra finch (*Taeniopygia guttata*), a highly social species in which only males
52 sing. Young zebra finches learn their song by listening, memorising and reproducing the song
53 of conspecifics, mainly adults (Derégnaucourt, 2011 but see Derégnaucourt & Gahr, 2013).
54 Song learning takes place during a sensitive period of the early life, between 25- and 90-days
55 post-hatch (dph), and past these 90 days, vocal changes are rarely observed (Immelmann, 1969).
56 In the zebra finch, song plays a crucial role in mate choice and the link between song and female
57 preference is well studied (for a review, see Riebel, 2009). Under natural conditions, each male
58 zebra finch has a unique song, which constitutes an individual signature (Clayton, 1988; Cynx
59 & Nottebohm, 1992) and is recognized by his sexual partner (Clayton, 1988). Female zebra
60 finches also have a sensitive phase for song preference learning (Riebel, 2003) and the
61 importance of subadult song experience in shaping adult song preferences has been well
62 demonstrated: if deprived of adult song during the sensitive phase of their early life, females
63 fail to discriminate differences in song quality and do not show consistent preferences as adults
64 (Lauay, Gerlach, Adkins-Regan, & DeVoogd, 2004; Riebel, 2000). Females, when adult, do
65 prefer the song they heard when they were young over other songs (Clayton, 1988, 1990; Miller,
66 1979a, 1979b; Riebel, 2009). In the wild, female mate choice is based on different signal
67 modalities, but it has been demonstrated that the song could potentially provide sufficient
68 information about a male for females to assess his quality and allow them to make their choice
69 (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.

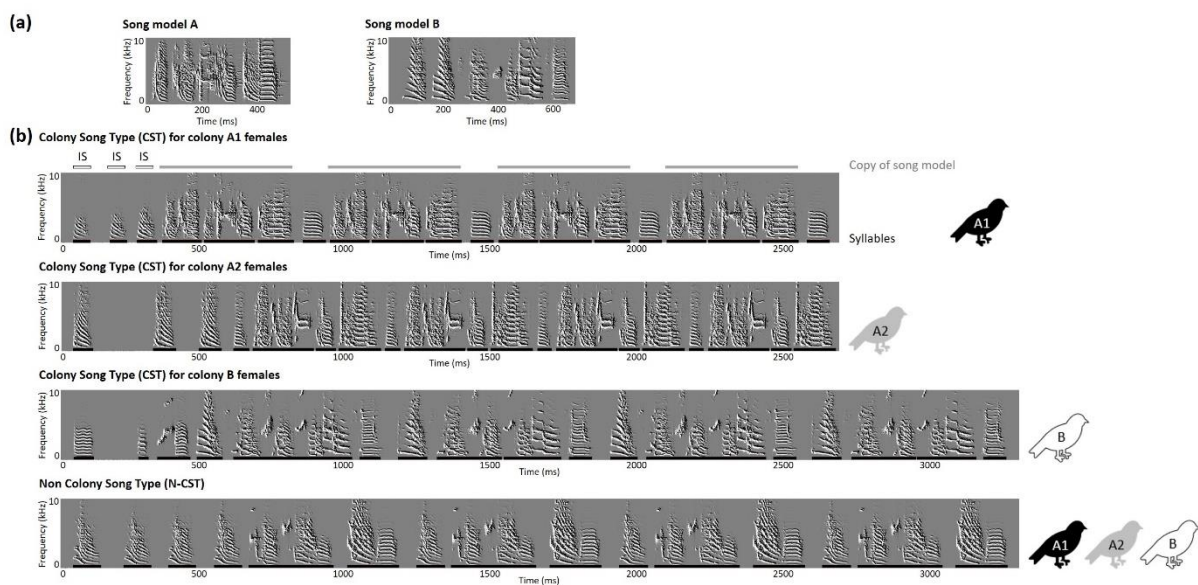
93 To verify this prediction, we tested female zebra finches with an operant conditioning
94 paradigm (Riebel, 2000; Riebel & Slater, 1998; Riebel, Smallegange, Terpstra, & Bolhuis,

95 2002; Salvin, Derégnaucourt, Leboucher, & Amy, 2018). During the test, a female had the
96 choice between two response keys, each triggering a different song type when pecked: one
97 response key triggered the playback of the song type of her colony, which we refer to as the
98 “Colony Song Type” (CST), and the other response key triggered the playback of a conspecific
99 song type that was different from the song type of her colony, which we refer to as the “Non-
100 Colony Song Type” (N-CST). According to our hypothesis, we expected that females would
101 peck more often on the response key triggering the CST than on the key triggering the N-CST.

102 **Materials and Methods**

103 **Subjects and rearing conditions**

104 All subjects in this experiment were adult female zebra finches that hatched and were
105 raised in our laboratory. Subjects originated from three different colonies, each of them founded
106 by males previously trained to produce the same song model (Le Maguer et al., under review).
107 Two colonies (colony A1 and colony A2) were founded by males singing song model A (Figure
108 1a). The third colony (colony B) was founded by males singing a different song model, song
109 model B (Figure 1a).



110

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

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

134 Details of how we set up colonies have been described elsewhere (Le Maguer et al.
135 under review). Briefly, founder males and founder females of each colony were housed together
136 in a communal aviary containing nest boxes and nesting material, so that they could reproduce
137 freely until we obtained at least 34 male pupils per colony. In colony A1, we obtained a total of
138 48 male and 27 female offspring after 346 days. In colony A2 we obtained 34 male and 26

139 female offspring after 399 days. In colony B we obtained 35 male and 37 female offspring after
140 555 days. Birds were individually marked with three coloured rings one of which was always
141 red and numbered. All birds that hatched in those three colonies (including females used for
142 this study) could interact freely with all the other birds of their colony. The three colonies were
143 kept in three different aviaries (3.18 x 3.32 x 2.84 m), visually and acoustically isolated from
144 each other so that the birds could not hear other songs than those produced by the males of their
145 own colony. All aviaries were set to a 14:10 light:dark (LD) schedule (lights on at 8 am - off at
146 10 pm) and maintained between 20 and 23°C. Birds had *ad libitum* access to water, seeds mix
147 and egg food for exotic finches, as well as sand and cuttlebones. The basic diet was
148 supplemented once a week with vegetables and fruits, and once a month with hard-boiled eggs.

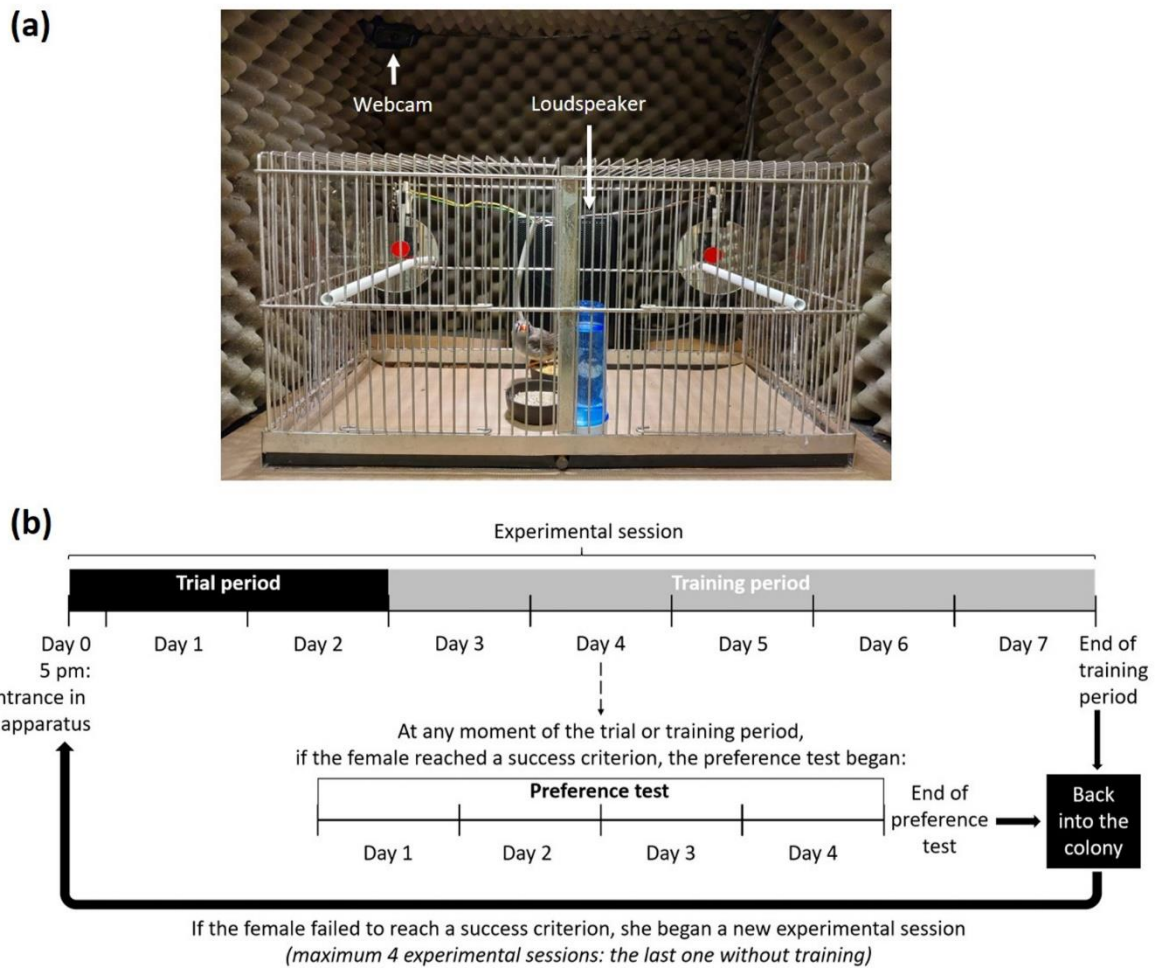
149 We tested a total of 63 females: 11 from colony A1, 21 from colony A2 and 31 from
150 colony B. Females from colony A1 were tested at the age of 1601 ± 86 days post-hatch (dph),
151 females of colony A2 at 792 ± 106 dph and females of colony B at 655 ± 89 dph.

152 Apparatus

153 We tested the preference of females for the dialect of their colony by using an operant
154 task with song as a reward (Riebel, 2000; Riebel & Slater, 1998; Riebel et al., 2002; Salvin et
155 al., 2018). The experimental set-up has been inspired by the one described in Houx & ten Cate
156 (1999) and used in other studies (Riebel, 2000; Riebel et al., 2002; Salvin et al., 2018). The
157 apparatus consisted of a sound-proof chamber (85 x 65 x 60 cm) containing a metal cage (46 x
158 22 x 26 cm) with two perches separated by 36 cm. A red response key (1 cm in diameter) was
159 placed above each perch. Behind each key, a mirror of 10 cm diameter was placed to reduce
160 the impact of social isolation. Seeds, egg food, water and sand were available *ad libitum*
161 throughout the experiment. When pecked, each red key triggered the playback of a song,
162 broadcasted via a loudspeaker (Yamaha MS101 III, Frequency Response: 30 Hz - 20 kHz)
163 located in between the two response keys. Songs were broadcast at a maximum amplitude of

164 70 dB at 30 cm from the speaker (Roline R0-1350 sound-level meter; fast response F and low
165 range LO, A settings). This level is comparable to that produced by a singing male (Houx &
166 ten Cate, 1999). Each sound-proof chamber was equipped with fans providing a low airflow
167 and OSRAM DULUX lights on an automatic 14:10 LD schedule.

168 After manually assigning one specific song to a particular key in SAP 2011 (Sound
169 Analysis Pro software; Tchernichovski, Lints, Derégnaucourt, Cimenser, & Mitra, 2004), this
170 software controlled the playback and automatically switched songs between the two keys each
171 night, to control for possible side preferences. The software kept track of all key pecks (number
172 of pecks and identity of the key pecked) and stored this information in My SQL Workbench 6.3
173 CE tables, from which we could extract excel files. This allowed us to track females' progress
174 day by day. Response keys were connected to the computer using a National Instruments USB-
175 6501 port. In order to check whether females intentionally pecked the keys during the test, each
176 sound-proof chamber was equipped with a Logitech C920 webcam. For a representation of the
177 experimental set-up, see Figure 2a.



178

179 **Figure 2.** Experimental apparatus and timeline. (a) Experimental set-up for the preference test.
 180 (b) Experimental timeline. Females were housed with members of their colonies until being
 181 transferred to soundproof chambers for the experimental session.

182 Stimuli

183 It has been demonstrated that female zebra finches are able to generalise their learnt
 184 preference for a specific song type (usually the father's song) to the songs of other unfamiliar
 185 males (Clayton, 1990; but see Riebel & Smallegange, 2003). Therefore, and in order to prevent
 186 an effect of familiarity in our experiment, both song types used as stimuli (CST and N-CST)
 187 were produced by unfamiliar birds. In a previous study we had conducted a detailed song
 188 analysis that revealed high similarities between males of colony A1 and colony A2 in song
 189 features such as syllable and element repertoire, song variability, inter-syllabic gap distribution

190 and song bout structure. At the same time, males from the colonies A1 and A2 differed from
191 those of colony B with respect to these song features (Le Maguer et al., under review). Thus,
192 we had created two different dialects: males from colony A1 and A2 sung one and the same
193 song dialect, males of colony B sung another dialect. The CST for A1 females were songs
194 produced by males of colony A2 and vice versa. Given the large number of males in these
195 colonies, a large pool of songs was available to create the song stimuli. In contrast, no such
196 second colony was available for females of colony B. Therefore, the CST for females of colony
197 B were songs of different males that had been trained to produce an imitation of the song model
198 B but that were not used as founder males for this colony. N-CST for females of the three
199 colonies were sung by males originating from the Max Planck Institute for Ornithology in
200 Seewiesen (Germany). Spectrographic illustrations of different stimuli that were used as a N-
201 CST are presented in Figure S1.

202 *Song recordings*

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

212 *Selection of songs based on the song model*

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

215 vocalisations that are separated from each other by silent gaps, and the motif is defined as a
216 short and stereotyped sequence of syllables (Figure 1b). To select song stimuli that best
217 represented the colony's song type, we chose songs from males that produced a very good copy
218 of the song model. To do so, we quantified a similarity score between the copy of the male and
219 the song model of his colony, using the song similarity procedure of SAP 2011 (Tchernichovski
220 et al., 2000; Le Maguer et al., under review). Males whose songs were chosen as CST stimuli
221 had a high similarity to the song model (mean \pm SD = 87 ± 8).

222 *Creation of song stimuli*

223 We first selected several song files per male which had a song that could serve as a CST
224 or a N-CST in one of the three colonies. Then, for each male, we selected one natural song bout
225 and digitally modified it using Avisoft SASLab Pro. The aim was to obtain song stimuli that
226 were of similar duration and to mimic the high acoustic stereotypy of natural directed songs
227 (Sossinka & Böhner, 1980). Thus, in the song bout of each male, we kept the three last
228 introductory syllables (preceding the first motif), followed by four renditions of the motif.
229 Depending on the male, we kept either the first song motif that was then copied three times, or
230 the first two song motifs that were then copied once. We kept the natural gap durations between
231 song motifs. To standardize all song stimuli, amplitude was root-mean square equalised with
232 Praat software (peak digitally scaled to 0.99).

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

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

249 Preference test

250 Each female subject was taken from her colony and transferred to the apparatus at
251 around 5 pm (day 0 of the experiment). From this moment on, the female had access to two
252 response keys and could hear the two different song types (N-CST and CST) sung by two
253 unfamiliar males, each one being triggered by one of the response keys. The females had
254 permanent access to the keys, but pecking the keys elicited songs only during the day: from 8
255 am when the lights switched on, to 10 pm when the lights switched off. As females had to learn
256 how to peck the keys, the first experimental session started with a trial period of two days (day
257 1 and day 2 of the experiment). A female could learn to peck the keys by autoshaping after she
258 accidentally pecked a key. We considered that a female had learned the task if we detected at
259 least 10 pecks on each key in one day (first learning criterion). The day on which this success
260 criterion was reached was considered day 1 of the preference test. Following day 1 of the
261 preference test, females had access to the keys during the three following days (day 2, 3 and 4
262 of the preference test), before transferring her back to her colony. Thus, the preference test
263 lasted four full days and assignment of stimuli to response keys was reversed each night, in
264 order to control for side preferences: on two days the CST was triggered by the right key, and

265 on two days the CST was triggered by the left key. Females that had not started to regularly
266 peck the keys at the end of the trial period (morning of day 3 of the experiment) underwent a
267 training procedure.

268 The training period lasted a maximum of five days (from day 3 to day 7 of the
269 experimental session) and consisted of two daily reinforcement sessions. Reinforcement was
270 provided by 1) drawing the attention of the female to the keys by manually pushing each key
271 several times when she was watching, and 2) sticking seeds or nesting material to the response
272 keys to enhance the appeal of the keys. We kept track of the pecks realised by females after
273 each reinforcement session. If a female still had not started to regularly peck the keys at the end
274 of the five-days training period (day 7 of the experiment), she was transferred back to her colony
275 where she rested for at least a week before a second identical experimental session started.
276 Some females exhibited a side preference that could not be overturned by temporarily hiding
277 the preferred key (i.e. the key on which they pecked more often) and reinforcing the non-
278 preferred key during the training period. We assumed that with the preferred key covered,
279 females would start to peck the non-preferred key and would continue to do so even after
280 uncovering the previously preferred key. However, this was not the case. In Figure S2, we
281 present a comparison of song preferences to side preferences at the colony level. For females
282 exhibiting a side preference, we considered that they learned how to peck a key if they pecked
283 the preferred key at least 20 times a day (second learning criterion). If a female failed to reach
284 one of the two learning criteria during the second experimental session, she underwent a third
285 experimental session after having spent at least a week in her colony.

286 If during one of the training sessions, the female started to regularly peck on both, or on
287 one particular key, training was stopped. The day that the female reached one of the two
288 learning criteria without any reinforcement was considered day 1 of her preference test. From
289 day 1 on, the test continued until day 4. Some females did not learn to press the keys during the

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

296 Notes on animal studies

297 All procedures reported here followed the European regulations on animal
298 experimentation and were approved by the French Ministry for National Education, Higher
299 Education and Research (authorization no. 02609.02).

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

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

320 Analysis

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

328 To analyse the females’ preferences, we calculated their preference ratio for the CST:
329 total number of pecks for the CST during the four days of test, divided by the grand total of
330 pecks over the four days period. We also calculated preference strength as the number of pecks
331 for the preferred song type, divided by the number of pecks for the less preferred song type.

332 Statistical analysis

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

339 whether the mean preference ratio was greater than chance by comparing it to 0.5 using a one-
340 sample t-test. We corrected p-values for multiplicity using the false discovery rate correction.
341 To check whether a link existed between motivation and preference strength, we used
342 Spearman's correlations because data were not normally distributed.

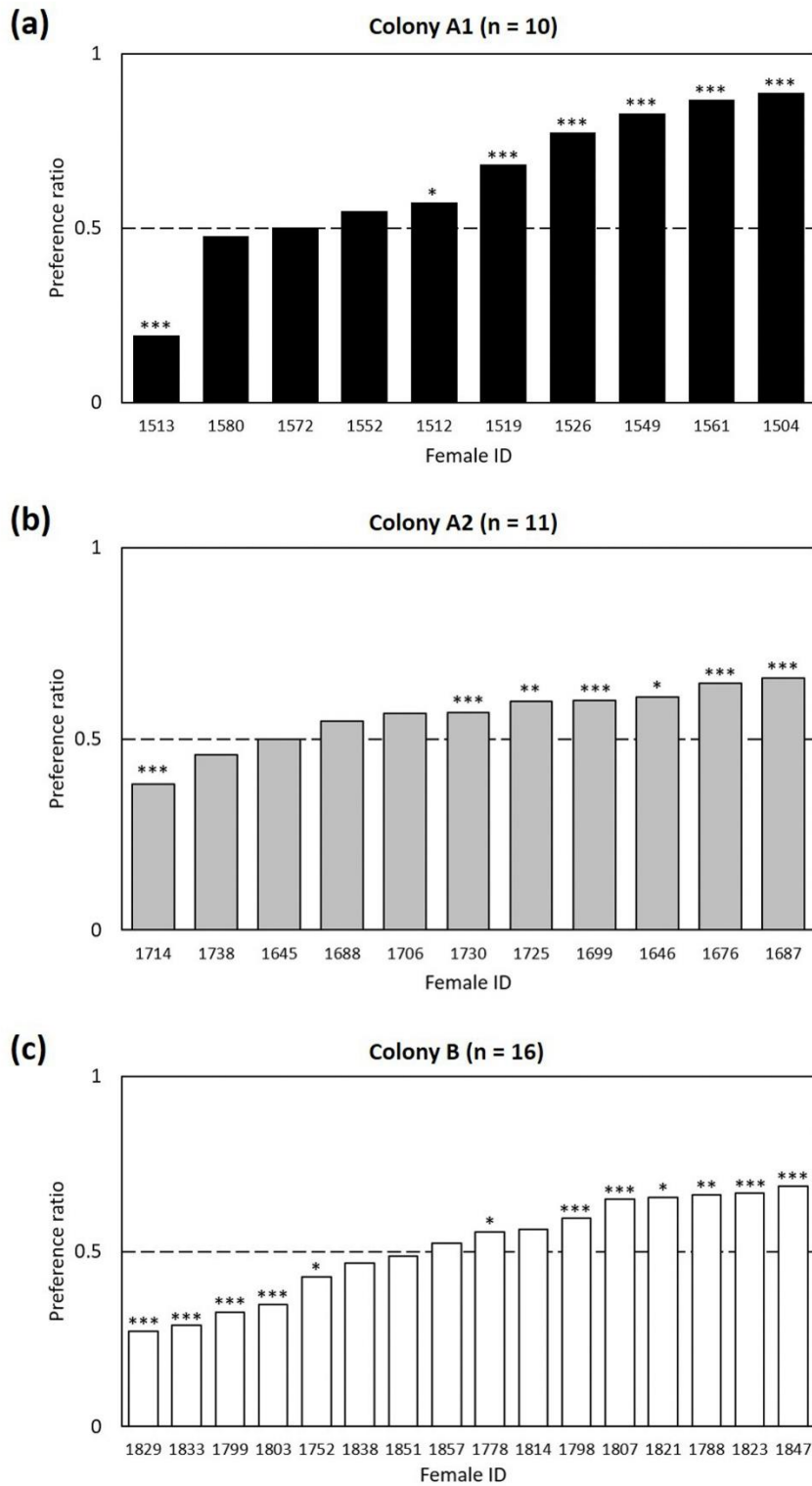
343 Finally, we tested whether the behavioural responses during the preference test differed
344 between the three colonies to check whether there was a higher preference ratio for the CST or
345 a higher number of pecks during the test in one of the three colonies. We ran two separate
346 generalized mixed models (GLMMs), one for each of the response variables. The first model
347 tested whether the preference ratio for the CST differed according to the colony and the second
348 model tested whether the total number of pecks differed between colonies. Both models
349 included the number of experimental sessions that the female needed to reach either of the two
350 learning criteria (i.e. whether she was successful in the 1st, 2nd, 3rd or 4th experimental session)
351 as a fixed effect. This variable is later referred to as "sessions to success". Both models included
352 the number (ID) of the set of song stimuli the female was tested with, as a random effect. Due
353 to high collinearity between the variables "female age" and "colony" we could not include
354 female age in the model. Thus, we kept only the variables "colony" and "sessions to success"
355 (there was no collinearity between these two variables). We used error distributions from the
356 quasi family as we detected overdispersion in both models. To test the preference ratio for the
357 CST, we used a GLMM with a quasibinomial distribution and a logit link function. For each
358 female (N = 37), the response variable was weighted by the total number of pecks she made
359 during the four days of test (using the *weights* parameter). For the total number of pecks, we
360 used a GLMM with a quasipoisson distribution and a log link function. Both models were
361 performed using the *glmmPQL* function from the *MASS* package in R. The levels of each
362 explanatory factor (i.e. "colony" and "sessions to success ") were compared to each other by
363 computing post-hoc Tukey tests with the *emmeans* package in R (Lenth, 2018).

364 **Results**

365 41 out of 63 tested females reached one of the two learning criteria. Four females pecked
366 the keys less than 20 times on the second day of test. Those four females were thus excluded
367 from the analysis. Therefore, the results for 37 females were used for further analysis (colony
368 A1: n = 10; colony A2: n = 11; colony B: n = 16). 15 out of these 37 females passed the
369 preference test during the first experimental session (colony A1: n = 3; colony A2: n = 5; colony
370 B: n = 7), three during the second experimental session (colony A2: n = 1; colony B: n = 2),
371 four during the third experimental session (colony A1: n = 3; colony B: n = 1), and 15 during
372 the fourth experimental session (colony A1: n = 4; colony A2: n = 5; colony B: n = 6) (Table
373 S3). For the number of successful females tested with each set of song stimuli, see Table S2.
374 Among the 37 females kept for analysis, some did not reach the first learning criterion due to
375 their preference for one particular key over the other – i.e. they pecked the non-preferred key
376 less often than 10 times a day (mean number of pecks per day \pm SD = 1 ± 2). However, they
377 did reach the second learning criterion. This side preference concerned 17 females: six in colony
378 A1, three in colony A2 and eight in colony B. In the preference analysis of these females, we
379 only focused on pecks on the preferred key and tested whether they pecked more often on the
380 preferred key when it was triggering the CST or when it was triggering the N-CST.

381 After calculation of each female's preference ratio (number of pecks for the CST/total
382 number of pecks), we witnessed that 26 out of the 37 females significantly preferred one of the
383 two song types, i.e. their preference ratio was significantly different from 0.5 (Figure 3). This
384 means they expressed a significant preference for one of the two song types that could be either
385 the CST or the N-CST (colony A1: 7 out of 10, colony A2: 7 out of 11, colony B: 12 out of 16;
386 Figure 3, Table 1 & Table S3). Additionally, among those 26 females out of 37 that showed a
387 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

393 1 indicate a preference for the CST, preference ratios approaching 0 indicate a preference for
 394 the Non-Colony Song Type (N-CST). Asterisks (*) indicate a significant preference for one of
 395 the two song types (see Table 1 and Table S3).

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

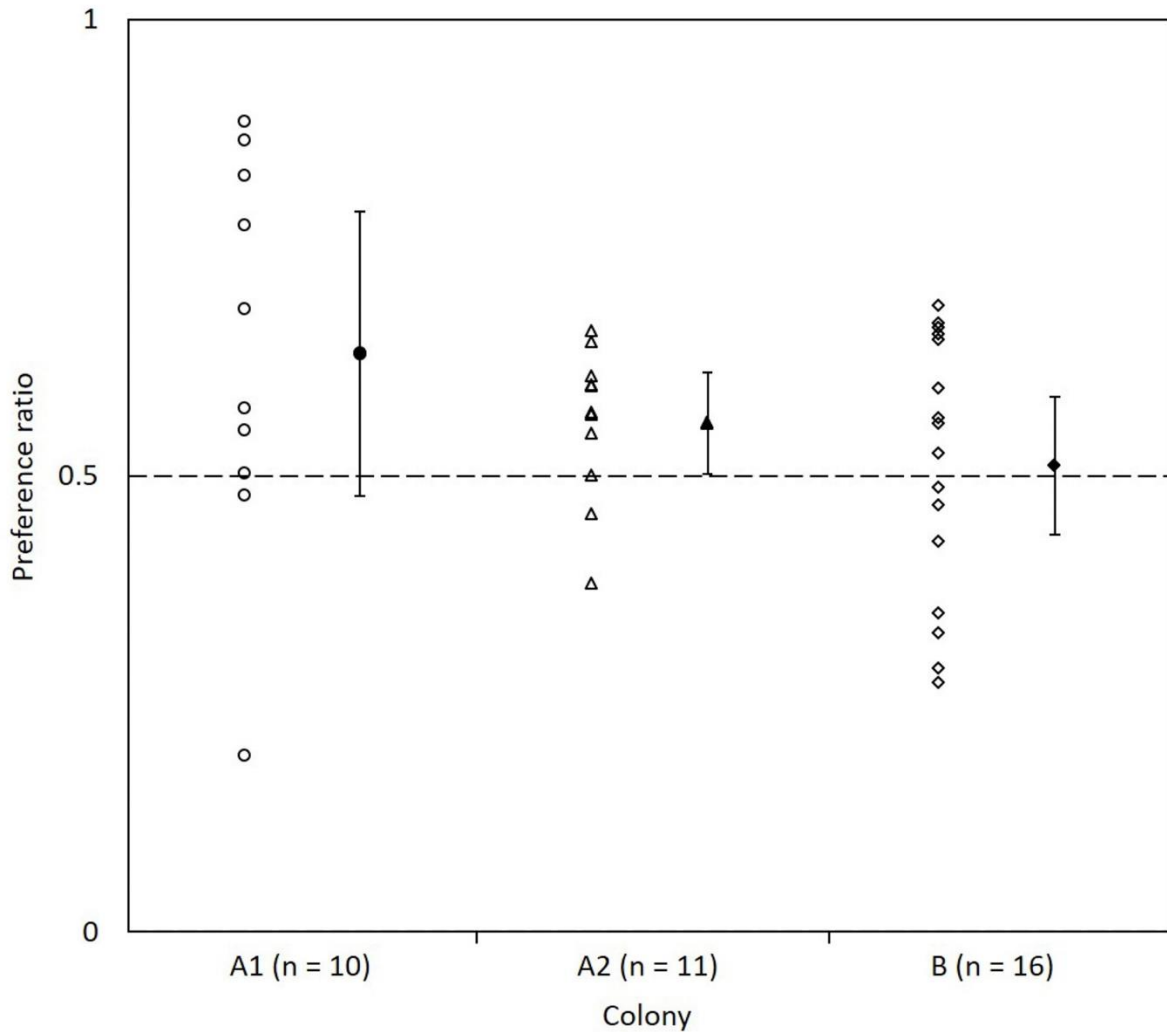
Colony	n		Females without a preference	Females with a preference		
				For the CST	For the N-CST	Total
A1	10	<i>n</i>	3	6	1	7
		%	30	60	10	70
A2	11	<i>n</i>	4	6	1	7
		%	36	55	9	64
B	16	<i>n</i>	4	7	5	12
		%	25	44	31	75

399

400 However, this preference for the colony song type was not reflected at the colony level.
 401 The preference for the CST was only significant in colony A2 (tested as a deviation from a 0.5
 402 preference ratio with one-sample t-test: $t = 2.30$, $df = 10$, $p = 0.044$; Figure 4). However, this
 403 significant difference disappeared when correcting for multiple testing ($p_{adjusted} = 0.126$). In
 404 colony A1 and B, the mean preference ratio was not significantly different from chance level
 405 of 0.5 (colony A1: $t = 1.94$, $df = 9$, $p = 0.084$, $p_{adjusted} = 0.126$; colony B: $t = 0.31$, $df = 15$, $p =$
 406 0.762 , $p_{adjusted} = 0.762$; Figure 4).

407

408



409

410 **Figure 4.** Preference ratio for the Colony Song Type (CST) over the Non-Colony Song Type
411 (N-CST) in each colony. Open symbols represent preference ratios of individual females. Filled
412 symbols represent the mean preference ratio (with 95% confidence interval). Preference ratios
413 approaching 1 indicate a preference for the CST, preference ratios approaching 0 indicate a
414 preference for the N-CST. The mean preference ratio was only significantly different from a
415 0.5 preference ratio (dashed line) in colony A2 (one sample t-test, $p = 0.044$). This significant
416 difference disappeared when correcting for multiple testing ($p_{adjusted} = 0.126$).

417 The absolute number of key pecks over the four days of test varied highly between
418 females (Table S3). In order to investigate a possible link between motivation and preference,

419 we tested whether females that pecked more often also had stronger preferences. However,
420 there was no significant correlation between the total number of key pecks and preference
421 strength in any of the colonies (colony A1: $r_s = 0.139$, $p = 0.707$; colony A2: $r_s = -0.073$, $p =$
422 0.839 ; colony B: $r_s = 0.444$, $p = 0.087$).

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

437 Table 2. Tukey post-hoc pairwise comparisons for GLMMs on the preference ratio for the
 438 Colony Song Type (CST) and on the total number of key pecks during the four days of
 439 preference test. Colony and number of experimental sessions needed to reach either of the two
 440 learning criteria ("sessions to success") are fixed factors. Significant differences are in bold. df
 441 = 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	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

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).

453 Our results are consistent with several previous studies which showed that females of
454 this species prefer the song they experienced during their early life (for a review, see Riebel,
455 2009). However, the current study differs from those earlier studies that usually gave females
456 a choice between the song of an unfamiliar male and a familiar one, such as the father's song,
457 the tutor's song or a song heard from playback during the sensitive phase of song preference
458 learning (Clayton, 1988; Miller, 1979a; Riebel, 2000; Riebel et al., 2002). The fact that many
459 females still preferred the CST over the N-CST even if it was sung by an unfamiliar individual,
460 suggests that this learned preference was strong enough to be generalised to an unfamiliar
461 songster. This confirms the females' ability to generalise the learnt song preference to songs of
462 unfamiliar males, an ability already demonstrated for zebra finches (Clayton, 1990; Riebel,
463 2009).

464 Even if some weak geographical variations in the song had been described in Australian
465 populations of zebra finches (Zann, 1993), the salience of these variations to females have not
466 been studied so far. Based on artificially created dialects of laboratory colonies, we were able
467 to show here that these acoustic variations matter to female zebra finches. The significance of
468 local song dialects to females for mate choice decisions has been investigated in other species
469 exhibiting geographical song variations naturally. For example, female Nuttall's white-crowned
470 sparrows (*Zonotrichia leucophrys nuttalli*) were more stimulated by male song of their natal
471 dialect than by male song of adjacent dialects (Baker, 1983). According to the “genetic
472 adaptation hypothesis” we propose that song dialects might matter to female zebra finches in
473 the context of mate choice, as a cue for assortative mating (Tomback & Baker, 1984). In other
474 words, pairing with a male singing the local song type would ensure the female that her
475 offspring will be genetically adapted to the local environment and will have a better survival
476 and reproductive success than foreign birds (Marler & Tamura, 1962, 1964; Nottebohm, 1969,
477 1972; Payne, 1981). Furthermore, it has been argued that female preferences play an important

478 role in the stability of song dialects (reviews in Baker & Cunningham, 1985; Payne, 1981;
479 Rothstein & Fleischer, 1987). In the brown-headed cowbird (*Molothrus ater*) females show
480 sexual preferences for the correct local whistle type, which could create a selection pressure on
481 males to conform to the local song type and could influence the stability of dialects (O’Loughlen
482 & Rothstein, 1995, 2003). The brown-headed cowbird is an interesting case as it is a brood
483 parasitic species in which young birds are not exposed to conspecific song during their early
484 life. Several studies in the zebra finch proposed that male song learning may likewise be
485 influenced by females. For instance, young males imitate a tutor song better when housed with
486 a hearing female than when housed without a female (Adret, 2004) and worse when housed
487 with a deaf female than when housed with a hearing female (Williams, 2004). More recently,
488 another study suggested that the process of song learning in young males could be guided by
489 the social feedback of an adult female zebra finch (Carouso-Peck & Goldstein, 2019). Given
490 that in the current study females mostly preferred songs of their home dialect, female
491 preferences might have played a role in the establishment and stability of artificial song dialects
492 in our colonies of zebra finches. That is, females’ preferences for the CST might have guided
493 young males to conform to this song model.

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

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

507 Despite the individual preferences of females for the CST, this preference was not
508 reflected at the colony level. Moreover, some females exhibited significant preferences for the
509 N-CST. In other species such as canaries (*Serinus canaria*), females exhibit clear preferences
510 for particular song syllables (Vallet & Kreutzer, 1995). However, there is no convincing
511 evidence so far that female zebra finches exhibit preferences for particular song features. It
512 rather seems that experience-dependent song preferences of a female zebra finch might
513 interplay with song features of the male's song (such as syllable diversity and spectro-temporal
514 details) to determine which song that female finds attractive (Riebel, 2009). Nevertheless, we
515 cannot exclude that some females in the current study preferred certain N-CST stimuli because
516 of particular sound characteristics.

517 One could have expected an effect of the number of experimental sessions needed to
518 reach either of the two learning criteria on the preference strength for the CST and the activity
519 level of females. This was not the case, suggesting that the rapidity with which a female learned
520 the operant task was not related to her preference strength or her motivation to peck the keys.
521 However, we did find some differences between the colonies in the preference ratio for the CST
522 and in the activity levels of females during the test. Females of colony A1 exhibited a higher
523 preference ratio for the CST and a higher number of pecks than females of colony B. This is
524 probably not due to the nature of the song dialect (A or B), as females of colony A2 and B did
525 not differ in those variables. It has been reported that experiences of females during adulthood
526 could influence their song preferences (e.g. in canaries, Béguin, Leboucher, & Kreutzer, 1998;
527 Nagle & Kreutzer, 1997). In zebra finches, females can develop preferences as adults (Clayton,

528 1988; Miller, 1979b; Riebel, 2009). Thus, we could assume that our females' adult experiences
529 with song affected their preference strength. Given that our females were housed with males
530 during their whole lives, we propose that the experience with the song type of males and the
531 ability for females to interact with them reinforced the previously learned preference. When
532 tested, females of colony A1 were much older than females of colony B. Therefore, they had
533 more experience with the CST, which could have resulted in a stronger preference for the CST
534 and a higher motivation to hear it.

535 In zebra finches, the lack of seasonality in breeding (Immelmann, 1968; Zann, 1996)
536 raises some issues concerning the nature of the observed preferences in females. In our study
537 we did not test for female sexual receptivity. Therefore, we wonder whether females that
538 showed a preference for the CST expressed a sexual preference related to mate choice, or a
539 social preference. In social species, shared song types favour group cohesion (Hausberger et
540 al., 2008). Accordingly, song could be interpreted as an affiliative signal rather than a mere
541 sexual signal in such species. Such social preferences could have played a role in our study as
542 well. To assess this possibility, a social learning task could be used in the future. In zebra
543 finches, the classical observer-demonstrator paradigm has been proven effective to assess social
544 learning in a context of food choice (Benskin, Mann, Lachlan, & Slater, 2002; Guillette &
545 Healy, 2014; Katz & Lachlan, 2003; Riebel, Spierings, Holveck, & Verhulst, 2012). Therefore,
546 if song dialects do constitute a social marker, an observer might preferentially learn his food
547 choice from a bird singing the CST than from a bird singing the N-CST. Female as well as male
548 zebra finches could be tested as observers to determine whether song dialects could constitute
549 an affiliative signal in this species.

550 In conclusion, our work expands on numerous studies showing that zebra finch females
551 express a preference for the song they heard early in life but is the first to demonstrate a direct
552 link between song dialects and female preference in this species. Our findings also underline

553 the difficulty of concluding on whether expressed female preferences in zebra finches are more
554 related to a social or to a sexual preference, but they pave the way to investigate whether song
555 dialects can be used as an affiliative signal in the context of social learning in this model species.

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562 **References**

- 563 Adret, P. (2004). Vocal imitation in blindfolded zebra finches (*Taeniopygia guttata*) is
564 facilitated in the presence of a non-singing conspecific female. *Journal of Ethology*,
565 22(1), 29-35. doi: 10.1007/s10164-003-0094-y
- 566 Baker, M. C. (1983). The behavioral response of female Nuttall's White-crowned Sparrows to
567 male song of natal and alien dialects. *Behavioral Ecology and Sociobiology*, 12(4),
568 309-315. doi: 10.1007/BF00302898
- 569 Baker, Myron Charles, & Cunningham, M. A. (1985). The Biology of Bird-Song Dialects.
570 *Behavioral and Brain Sciences*, 8(1), 85-100. doi: 10.1017/S0140525X00019750
- 571 Beecher, M. D., Campbell, S. E., & Nordby, J. C. (2000). Territory tenure in song sparrows is
572 related to song sharing with neighbours, but not to repertoire size. *Animal Behaviour*,
573 59(1), 29-37. doi: 10.1006/anbe.1999.1304
- 574 Béguin, N., Leboucher, G., & Kreutzer, M. L. (1998). Sexual Preferences for Mate Song in
575 Female Canaries (*Serinus Canaria*). *Behaviour*, 135(8), 1185-1196. doi:
576 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

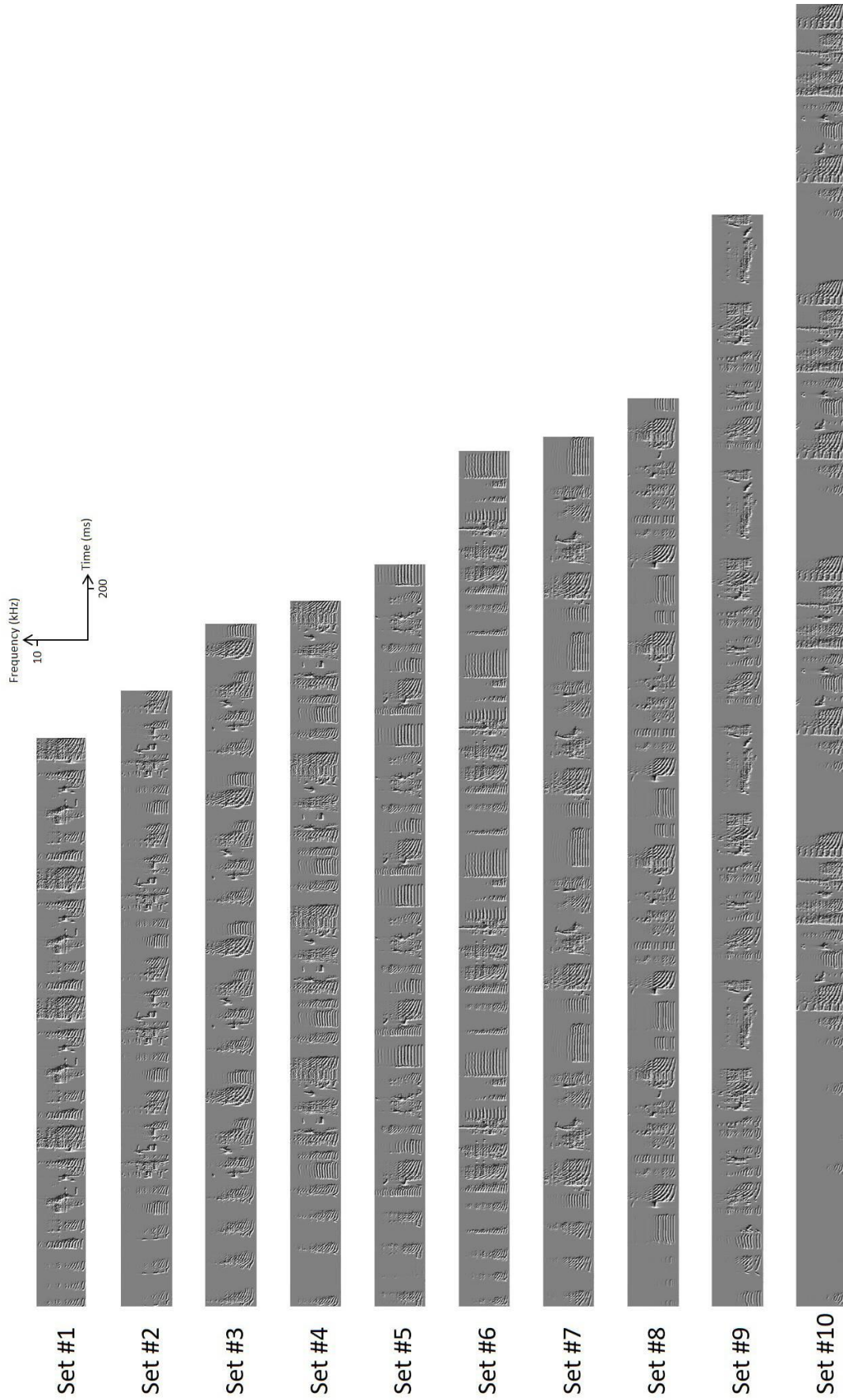
734 Tomback, D. F., & Baker, M. C. (1984). Assortative mating by white-crowned sparrows at song
735 dialect boundaries. *Animal Behaviour*, 32(2), 465-469. doi: 10.1016/S0003-
736 3472(84)80282-1

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



756 **Figure S1. Spectrograms of songs used as a Non-Colony Song Type (N-CST) stimulus.**
757 There was a different N-CST stimulus in each set of song stimuli (a set was composed of one
758 N-CST stimulus and three Colony Song Type (CST) stimuli; one for females of each colony).
759 The 10 N-CST stimuli were recorded from 10 different adult males originating from the Max
760 Planck Institute for Ornithology in Seewiesen (Germany).

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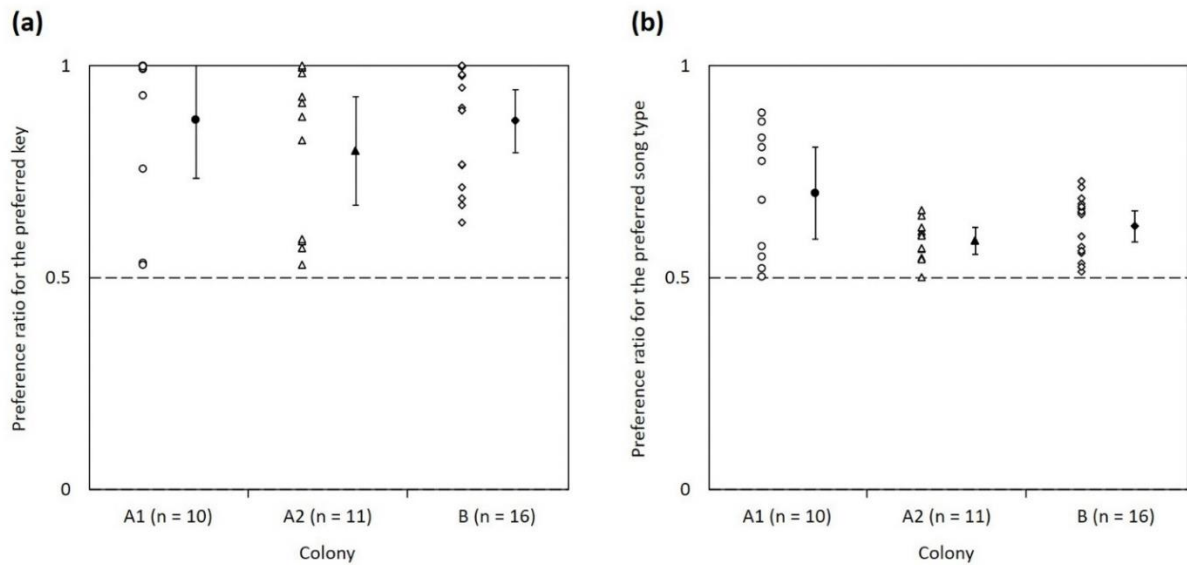
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769 **Comparison of song preference vs. side preference**

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



783 **Figure S2. Comparison of side preferences and song preferences in each colony.** Open
 784 symbols represent individual females' preference ratios. Filled symbols represent the mean
 785 preference ratio (with 95% confidence interval). (a) Preference ratio for the preferred key over
 786 the non-preferred key. The mean preference ratio was significantly different from a 0.5
 787 preference ratio (dashed line) in all colonies (colony A1: $t = 6.06$, $df = 9$, $p < 0.001$, $p_{adjusted} <$
 788 0.001 ; colony A2: $t = 5.2$, $df = 10$, $p < 0.001$, $p_{adjusted} < 0.001$; colony B: $t = 10.6$, $df = 15$, $p <$
 789 0.001 , $p_{adjusted} < 0.001$). (b) Preference ratio for the preferred song type over the non-preferred
 790 song type. The mean preference ratio was significantly different from a 0.5 preference ratio
 791 (dashed line) in all colonies (colony A1: $t = 4.16$, $df = 9$, $p = 0.0024$, $p_{adjusted} = 0.0024$; colony
 792 A2: $t = 6.09$, $df = 10$, $p < 0.001$, $p_{adjusted} < 0.001$; colony B: $t = 6.99$, $df = 15$, $p < 0.001$, $p_{adjusted}$
 793 < 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	-

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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

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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	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	

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