

1 **Breeding Experience and not Age Modulates the Song**
2 **Development of Pied Flycatchers (*Ficedula hypoleuca*)**

3

4

5 Alba Motes-Rodrigo^{*}, Antonieta Labra^{*,†} and Helene M. Lampe^{*}

6

7 ^{*} Department of Biosciences, Centre for Ecological and Evolutionary Synthesis.
8 University of Oslo. Norway

9

10 [†] Laboratorio de Neuroetología. Programa de Fisiología y Biofísica, Instituto de
11 Ciencias Biomédicas, Facultad de Medicina, Universidad de Chile, Chile.

12

13 **Correspondence:** H. M. Lampe. Department of Biosciences, Centre for Ecological
14 and Evolutionary Synthesis. University of Oslo. Norway. E-mail:
15 h.m.lampe@ibv.uio.no

16

17

18 **Abstract**

19 In songbirds, the development of the species-specific adult song involves a learning
20 process that varies in extension. In species that incorporate new song elements
21 throughout life (open-ended learners), variation in male song composition could be
22 the result of either age or breeding experience. Using data from 16 years of fieldwork
23 on pied flycatchers (*Ficedula hypoleuca*) we aimed to disclose the individual
24 contribution of these two factors on the species song characteristics, as well as their
25 relation with morphology and plumage color changes. Finally, we explored if any of
26 the song or physical features could predict the probability of males returning to the
27 breeding site. We found that the song characteristics of the first time breeders did not
28 differ between age classes, except for the total number of syllables per song, which
29 was higher in the 1-year old than the 2-years old males. However, we found that song
30 variables associated with complexity (song and sample versatilities and repertoire
31 size), increased significantly from the first to the second breeding season. Males
32 showed delayed plumage maturation, with 1-year old males being browner than the 2-
33 years old males independently of their breeding experience. Morphology, however,
34 was not affected by age or breeding experience. The probability that males returned to
35 the breeding site was not associated with song or physical features. We discuss the
36 consequences and implications of breeding experience, rather than age, accounting for
37 male song variation.

38

39

40 Key words: song learning, delayed maturation, plumage color, morphology, song
41 repertoire, survival.

42

43 **Introduction**

44 Bird songs are among the most beautiful and impressive sounds of nature. Songs are
45 vocalizations which have a tonality and a rhythm (Spector 1994), usually defined as
46 long utterances used for defending a territory and attracting a mate during the
47 breeding season (Catchpole & Slater 1995). In the temperate zone it is usually males
48 who sing and some of their song characteristics could be understood as “an acoustic
49 equivalent of a peacock tail” (Catchpole 1987) and thus, be a target of sexual
50 selection. The evolution of these complex repertoires has been mainly discussed using
51 the “mate choice hypothesis”, which predicts that females of songbirds would prefer
52 males with larger song repertoires (Searcy & Yasukawa 1996; but see also Byers &
53 Kroodsma 2009).

54 The process of developing the species-specific adult song is highly complex, and
55 involves two phases: memorization and rehearsal (Marler 1970a; Slater 1989; Konishi
56 1994; Catchpole & Slater 1995; Nowicki et al. 1998). In the memorization phase,
57 song is learned from a tutor (Marler 1970a; Marler & Slabbekoorn 2004). In zebra
58 finches (*Taeniopygia guttata*) for example, this phase usually takes place during a
59 short period that begins one to two weeks after hatching and lasts for about 30-60
60 days (Immelmann 1969; Roberts et al. 2012). In the second phase, the rehearsal or
61 motor phase, birds adjust their songs to match what they learned previously. In early
62 stages of the phase, birds sing amorphous songs (subsongs) that develop later on into
63 more variable songs (plastic songs), which finally evolve into stereotyped
64 (crystalized) copies of the model they memorized earlier (Marler 1990; Bolhuis &
65 Gahr 2006). Individuals that do not have a model to imitate produce abnormal songs
66 when they become adults (Thorpe 1958; Nottebohm 1968).

67 Songbird species vary in the length of these two phases of the learning period
68 (Marler & Slabbekoorn 2004). On the one hand, the age-limited or close-ended
69 learner species, have a learning window limited to the first year of life and are not
70 able to learn new song elements after the crystallization period (Marler 1990), as in
71 the case of song sparrows (*Melospiza melodia*; Nordby et al. 2002) and zebra finches
72 (Böhner 1990). On the other hand, open-ended learners can learn new songs rather
73 continuously throughout life by incorporating new song elements (Marler 1990). They
74 have high vocal plasticity and their song changes with age and often their repertoire
75 size is smaller in yearlings (Kipper & Kiefer 2010), as in nightingales (*Luscinia*
76 *megarhynchos*; Kiefer et al. 2006) and canaries (*Serinus canaria*; Lehongre et al.
77 2006).

78 The existence of smaller repertoires in younger males has been explained by the
79 delayed song maturation hypothesis (Cucco & Malacarne 2000; Poesel & Nelson
80 2012). Accordingly, younger males would benefit from having a limited song
81 repertoire as this may lead to less competition with older males. A similar
82 phenomenon occurs regarding male plumage color. In this case, delayed plumage
83 maturation refers to clearly distinguishable male plumage features between the 1-year
84 old and adult individuals, thus 1-year old males resemble physically females although
85 they are sexually mature (Rohwer et al. 1980; Hawkins et al. 2012). Furthermore, it
86 has been suggested that the main differences in plumage color maturation can be
87 observed between 1-year old and older males (Cucco & Malacarne 2000). Thus,
88 plumage and songs seem to respond to similar selective pressures, as Cucco and
89 Malacarne (2000) found for the species from which data was available; delayed song
90 maturation was associated with delayed plumage color maturation.

91 Previous data, thus, provide clear evidence that for different open-ended learner
92 species, age is a determining factor of male song variation (Kipper & Kiefer 2010).
93 However, there are different patterns to when the learning process takes place. There
94 are species which songs change only from year 1 to 2, as can be observed in
95 nightingales (Kiefer et al. 2006; Kipper & Kiefer 2010), banded wrens (*Thryothorus*
96 *pleurostictus*, Vehrencamp et al. 2007), collard flycatchers (Garamszegi et al. 2007),
97 and whitethroats (*Sylvia communis*; Balsby 2000; Balsby & Hansen 2010). In
98 contrast, there are species that change their songs years after, such as barn swallows
99 (*Hirundo rustica*, Galeotti et al. 2001), sedge warblers (*Acrocephalus*
100 *schoenobaenus*, Nicholson et al. 2007), and pied flycatchers (*Ficedula hypoleuca*,
101 (Lundberg & Alatalo 1992; Espmark & Lampe 1993; Eriksen et al. 2011;
102 Vabishchevich 2012).

103 Breeding experience may be another relevant factor to explain male song variation
104 in open-ended learners since songs are learned from neighbors during the breeding
105 season (Lundberg & Alatalo 1992; Kiefer et al. 2009; Kipper & Kiefer 2010), but the
106 individual contribution of age and breeding experience is not yet clear. For that
107 reason, in the present study we aimed to assess if known-age male pied flycatchers
108 increase their repertoires as well as other song variables, as they become older or
109 more experienced breeders. In this species, differences in song characteristics across
110 individuals can be highly relevant for female choice. Females are more attracted to
111 males that sing larger and more complex repertoires (Lampe & Sætre 1995) and
112 repertoire size has been suggested to be a sign of territory quality (Lampe & Espmark
113 2003). In addition, repertoire size correlates with the arrival order, experience, body
114 mass, condition and plumage color (Lampe & Espmark 1994), and darker males are
115 preferred by females (Sætre et al. 1997). Moreover, males with higher song rate pair

116 earlier, suggesting that the song rate may be interpreted by females as indicative of
117 territory quality and/or male quality (Gottlander 1987).

118 Pied flycatcher is a long distance migrant and males that return to breed for the
119 first time can be either 1- or 2-years old (Lundberg & Alatalo 1992). For our study,
120 we first performed a cross-sectional comparison of these two age groups regarding
121 song and physical measurements to test if there were differences between 1- and 2-
122 years old. We also did a longitudinal comparison of the recordings of the individuals
123 that came back a second breeding season with their previous recordings and
124 measurements from their first breeding season, in order to identify differences due to
125 breeding experience. We further determined if song characteristics or physical
126 parameters are proxies of the probability that males return to the breeding site, by
127 comparing the returning and non-returning males. We expected that both age and
128 experience affect song performance, as songs that are more complex would be the
129 result of a longer exposure to tutors and of rehearsing with age or more breeding
130 experience.

131

132 **Methods**

133 Songs of pied flycatcher males were recorded before they were mated, during the
134 breeding seasons between 1997 and 2013. The breeding area is a mixed coniferous
135 forest at Sinober in Sørkedalen (59°59'N, 10°38'E, 160-200 m asl) near Oslo
136 (Norway), where wooden nestboxes are found at 30-50 m intervals. The approximate
137 dimensions of the nest boxes were 11 x 13 x 21 cm on the inside, 15 x 17 x 27 cm on
138 the outside, with a 3.5 cm diameter opening and 15 cm height to the opening. The
139 area was monitored every day to check the arrival of the males, which on average,
140 arrive a week before females (Lundberg & Alatalo 1992; Canal et al. 2012). After

141 recording them, males were captured in the nestbox they defended, and weighted to
142 the nearest 0.1 g with a Pesola spring balance. Tarsus length was measured with toes
143 bent from the extreme bending point at the inter-tarsal joint with a sliding caliper to
144 the nearest 0.5 mm. The plumage color was measured by comparing it with a Drost
145 color scale (Drost 1936), where I is completely black head and back and VII
146 completely brown. Males included in this study had been banded as nestlings with
147 uniquely numbered aluminum rings, but we also gave them two color rings on their
148 first capture as adults for easier identification if they returned in subsequent years.

149 Our study included 26 males that had hatched at the study site, and from which
150 acoustic and physical data were available. These males differed in their age when they
151 returned to the breeding site: 15 males were 1-year old and 11 males were 2-years old
152 (see Fig. 1). From the 26 males, 11 were captured and measured for two consecutive
153 breeding seasons, but for only seven were songs also recorded (see Fig. 1).

154 Songs were recorded using TC-D5 ProII Sony cassette recorders until 2007 and
155 had to be digitized. Thereafter, songs were recorded directly as digital files on
156 memory cards using Sound Devices 702 (sampling rate 44100 Hz, 24 bits) or Marantz
157 PMD661 MK11 (sampling rate 44100 Hz, 16 bits). Telinga PRO parabolic
158 microphones (Telinga Microphones, Sweden, frequency range 60-20000 Hz) were
159 used with all recorders. We recorded songs in the mornings during the most active
160 singing period (usually 07:00–12:00 h).

161 For each male, we analyzed a sample of 25 consecutive songs. The sound files
162 were analyzed using RAVEN pro version 1.4 (Cornell Laboratory of Ornithology,
163 Ithaca, NY), with a sample rate of 44100 Hz and 16-bit resolution and a discrete
164 Fourier Transformation size of 256 together with a sonogram overlap of 50%. From
165 direct visual inspection of the sonogram we determined the different syllables of each

166 song (Lundberg & Alatalo 1992). A syllable is a continuous song element or group of
167 elements separated from each other by more than 0.02 s (Fig. 2). If the separation is
168 more than 1 s, it is considered a new song. In total, seven variables were calculated
169 for each individual per breeding season based on variables that have been shown to be
170 important for female choice (Lampe & Espmark 2003).

171 1- Song duration, to the nearest 0.01 s.

172 2- Total number of syllables per song.

173 3- Total number of different syllables per song.

174 4- Total number of syllables in the whole sample (25 songs).

175 5- Syllable repertoire size, the total number of different syllables in the whole sample
176 (25 songs).

177 6- Song versatility. The ratio between 3 and 2: Total number of different syllables per
178 song/ Total number of syllables per song.

179 7- Sample versatility. The ratio between 5 and 4: Syllable repertoire size/ Total
180 number of syllables in the whole sample.

181 Two-tailed Student's t-tests for independent samples were conducted after testing
182 for normality in order to analyze if there were significant differences among the song
183 variables and physical measurements between (i) the 1- and 2-years old first time
184 breeding males and (ii) the males returning a second breeding season versus the non-
185 returning males. Two-tailed paired samples t-tests were used to analyze the
186 differences among song variables and physical measurements between the males
187 recorded in two consecutive breeding seasons. Bonferroni corrections were not
188 applied on significant data because of the controversy about its limitations in the field
189 of ecology and ethology (Perneger 1998; Moran 2003; Nakagawa 2004). Data was

190 analyzed with SPSS (IBM Analytics), statistical significance was set at $p < 0.05$ and
191 values are reported as Mean \pm SE.

192

193 **Results**

194 Song variables for individuals being 1- or 2-years old in their first breeding season
195 showed no significant differences except for the total number of syllables per song,
196 which was higher in the 1-year old males (Table 1). In addition, body mass and tarsus
197 length were similar between males of different ages, but plumage color was
198 significantly darker in the 2-years old males (Table 1).

199 The song parameters recorded during the first breeding season were similar
200 between those males that returned in a consecutive breeding season and those males
201 that did not return to the breeding site (Table 2). There were no significant differences
202 in morphology or plumage color between the returning and non-returning males
203 (Table 2).

204 The song variables of those males that were recorded in two consecutive breeding
205 seasons showed a significant increase between years for those variables associated to
206 complexity, i.e. sample and song versatility as well as repertoire size (Table 3).
207 Moreover, the latter almost doubled on average from the first to the second year (Fig.
208 3). Morphology and plumage color did not change between breeding seasons (Table
209 3).

210

211 **Discussion**

212 Repertoire size has been generally accepted to act as an indicator of male age in
213 open-ended learners (see Kipper & Kiefer 2010 for a review), but our results suggest
214 a different picture. Comparisons of the song variables of 26 known-age male pied

215 flycatchers banded as nestlings and subsequently recorded at the breeding site in their
216 first breeding season when either 1- or 2-years old, showed no significant effect of
217 age. However, the song characteristics associated with complexity differed between
218 the first and second time males were at the breeding site, and males almost doubled
219 their repertoire in the second season. Thus, our data indicate that for pied flycatchers
220 the males' breeding experience, instead of their age, is a determinant factor for their
221 repertoire size and other song characteristics revealing song complexity.

222 Some previous studies analyzing the changes in the songs of 1- and 2-years old
223 pied flycatchers also showed no variation between years (Espmark & Lampe 1993;
224 Eriksen et al. 2011), but these studies presented some limitations as the authors
225 included few 1-year old males (five in Eriksen et al. 2011) or assumed all first time
226 breeders to be 1-year old (Espmark & Lampe 1993). In our study, where we
227 controlled for the breeding experience, we found similarities in song characteristics
228 between males of the two age groups. These results differ however, from what has
229 been found in yearlings of the closely related collared flycatcher (*Ficedula albicollis*),
230 which had smaller repertoires than older males (Garamszegi et al. 2007). A key factor
231 to explain these differences may be the level of the analysis (Kiefer et al. 2009); while
232 we analyzed longitudinal changes, Garamszegi et al. (2007) analyzed cross-sectional
233 changes. In fact, both flycatcher species show an overall positive relationship between
234 repertoire size and age at the cross-sectional, population level (Lundberg & Alatalo
235 1992; Lampe & Espmark 1994; Garamszegi et al. 2007). Nevertheless, the type of
236 analyses seems not to be enough to explain variation in song development of pied
237 flycatchers. In a population of Russian pied flycatchers, some yearlings showed
238 delayed song maturation, while other yearlings did not, singing indistinguishable from
239 adult males (Vabishchevich 2012).

240 In our population of pied flycatchers, breeding experience significantly affected
241 the song variables associated with song complexity (repertoire size, sample and song
242 versatilities), as was indicated previously in common nightingales (Kiefer et al. 2009).
243 The biological significance of conveying the breeding experience through the song is
244 justified if some males do not return to the breeding site the first year after hatching,
245 remain in the wintering grounds instead of migrating north as is the case of the pied
246 flycatcher (Lundberg & Alatalo 1992). Independently of why males do not come
247 back, when they do return there would be an impairment between their age and their
248 breeding experience, as their breeding experience will be equivalent to that of
249 younger males. When this is the case, and since females prefer larger repertoires
250 (Lampe & Sætre 1995; Lampe & Espmark 2003), there might be a strong sexual
251 selection for song complexity to be an honest indicator of male breeding experience
252 rather than an exclusively age-dependent trait. A higher complexity in the songs may
253 inform the females that the singer already has the skill to find a good territory and
254 defend it, as males sing to attract females once they are ready to mate (Lundberg &
255 Alatalo 1992). The increased song complexity between the first two breeding seasons
256 implies that males learn new syllables from their neighbors that sing in the breeding
257 area (Lundberg & Alatalo 1992; Eriksen et al. 2011) and not in the winter grounds.
258 Previous studies indicate that pied flycatchers learn after the second breeding season
259 (Eriksen et al. 2011), but it remains unclear how much annual breeding experience
260 continues to modulate song characteristics after the second breeding season.

261 The pattern of song learning seems to be reflected in expected longevity since the
262 long-lived species learn new songs throughout their lives (an exception is the sedge
263 warbler that may only live to be six years old but still learn to new songs each year,
264 Cucco & Malacarne 2000). Both pied flycatcher and barn swallows have maximum

265 ages of around 15 years, while the nightingale and collared flycatcher may live to be
266 half that age (Cucco & Malacarne 2000).

267 The comparisons of the song parameters recorded the first breeding season
268 between the returning and non-returning males to the breeding site, did not show
269 significant differences. Previously a smaller repertoire size has been found in those
270 individuals that returned in another population of pied flycatchers (Lampe & Espmark
271 1994). Similarly, for song sparrows (Hiebert et al. 1989; but see Potvin et al. 2015)
272 and collared flycatchers (Garamszegi et al. 2007) song characteristics do not provide
273 information on the probability to return. Migratory behavior may explain if song
274 characteristics are proxies of the return rates. In partial migrants and resident
275 populations the song characteristics are positively associated with the return
276 rate/survival (great tit, McGregor et al. 1981; Lambrechts & Dhondt 1986; resident
277 song sparrow Hiebert et al. 1989), while long distance migrants show a negative
278 relationship (collared and pied flycatchers, Lampe & Espmark 1994; Garamszegi et
279 al. 2007) or no relationship as in migratory song sparrows (migratory song sparrows,
280 Potvin et al. 2015). Thus, in migratory species song may not be a reliable predictor of
281 male return rates or survival, as birds can be exposed to many different factors that
282 can prevent their returning. Furthermore, we did not find that physical measurements
283 would be proxies of the males' return rates.

284 The pied flycatcher shows delayed plumage maturation (Järvi et al. 1987), and in
285 agreement, we also found a significant difference in plumage color between 1-year
286 old and 2-years old males, which may reduce aggression from other males but
287 increase aggression from females (Slagsvold & Sætre 1991). In this context, increase
288 in the number of syllables per song may be a good strategy for the 1-year old males to
289 compensate for their plumage color, to make the song more attractive to females.

290 However, since the most important variables for attracting females are related to song
291 complexity (repertoire size, song and sample versatility; Lampe & Sætre 1995), and
292 these were similar for 1- and 2-years old males, it is unlikely that having more
293 syllables per song can counter the age effect. Alternatively, 1-year old males could
294 sing more syllables to increase the efficiency of territory defense, as was suggested to
295 occur for the song rate in collared flycatchers, where yearlings sing at higher rates and
296 respond more aggressively towards intruders than older males do (Garamszegi et al.
297 2006; Garamszegi et al. 2007). In the case of pied flycatcher, this is also an unlikely
298 hypothesis as males rarely evict other males, and song is primarily used in female
299 attraction (Lundberg & Alatalo 1992). It is more probable that the high number of
300 syllables per song sang at an early age may be equivalent to a “plastic phase” in the
301 motor phase of song learning, when males have more syllables in their songs and
302 rehearse the syllables that later on will constitute their repertoire (Marler 1970b).

303 To summarize, our results show that male pied flycatchers almost double their
304 repertoire size from their first to their second breeding season, suggesting that males'
305 song repertoires convey information about their breeding experience rather than their
306 age *per se*, which might play an important role in female choice. Finally, we did not
307 find evidence for song or physical features acting as a reliable predictor of a male's
308 return rate.

309

310 **Acknowledgements**

311 Authors are grateful to all the many field assistants that have helped with the
312 fieldwork during the years, including song recordings. A. M-R is grateful for her
313 Erasmus, NILS, UNIVEX, MECD and Obra Social La Caixa fellowships.

314

315 **Literature Cited**

- 316 Balsby, T. J. S. 2000: Song activity and variability in relation to male quality and
317 female choice in Whitethroats *Sylvia communis*. J. Avian Biol. **31**, 56-62.
- 318 Balsby, T. J. S. & Hansen, P. 2010: Element repertoire: change and development with
319 age in Whitethroat *Sylvia communis* song. J. Ornithol. **151**, 469-476.
- 320 Böhner, J. 1990: Early acquisition of song in the zebra finch, *Taeniopygia guttata*.
321 Anim. Behav. **39**, 369 -374.
- 322 Bolhuis, J. J. & Gahr, M. 2006: Neural mechanisms of birdsong memory. Nat. Rev.
323 Neurosci. **7**, 347-357.
- 324 Byers, B. E. & Kroodsma, D. E. 2009: Female mate choice and songbird song
325 repertoires. Anim. Behav. **77**, 13-22.
- 326 Canal, D., Jovani, R. & Potti, J. 2012: Multiple mating opportunities boost protandry
327 in a pied flycatcher population. Behav. Ecol. Sociobiol. **66**, 67-76.
- 328 Catchpole, C. K. 1987: Bird song, sexual selection and female choice. Trends Ecol.
329 Evol. **2**, 94-97.
- 330 Catchpole, C. K. & Slater, P. J. B. 1995: The study of bird song. Cambridge
331 University Press, Cambridge, UK.
- 332 Cucco, M. & Malacarne, G. 2000: Delayed maturation in passerine birds: an
333 examination of plumage effects and some indications of a related effect in
334 song. Ethol. Ecol. Evol. **12**, 291-308.
- 335 Drost, R. 1936: Über das brutkleid männlicher trauerfliegenfänger, *Musicapa*
336 *hypoleuca*. Vogelzug **6**, 179-186.
- 337 Eriksen, A., Slagsvold, T. & Lampe, H. M. 2011: Vocal plasticity- are pied
338 flycatchers, *Ficedula Hypoleuca*, open-ended learners? Ethology **117**, 188-
339 198.

- 340 Espmark, Y. O. & Lampe, H. M. 1993: Variations in the song of the pied flycatcher
341 within and between breeding seasons. *Bioacoustics* **5**, 33-65.
- 342 Galeotti, P., Saino, N., Perani, E., Sacchi, R. & Møller, A. P. 2001: Age-related song
343 variation in male barn swallows. *Ital. J. Zool.* **68**, 305-310.
- 344 Garamszegi, L. Z., Rosivall, B., Hegyi, G., Szöllösi, E., Török, J. & Eens, M. 2006:
345 Determinants of male territorial behavior in a Hungarian collared flycatcher
346 population: plumage traits of residents and challengers. *Behav. Ecol.*
347 *Sociobiol.* **60**, 663-671.
- 348 Garamszegi, L. Z., Török, J., Hegyi, G., Szöllösi, E., Rosivall, B. & Eens, M. 2007:
349 Age-dependent expression of song in the collared flycatcher, *Ficedula*
350 *albicollis*. *Ethology* **113**, 246-256.
- 351 Gottlander, K. 1987: Variation in the song rate of the male pied flycatcher *Ficedula*
352 *hypoleuca*: Causes and consequences. *Anim. Behav.* **35**, 1037-1043.
- 353 Hawkins, G. L., Hill, G. E. & Mercadante, A. 2012: Delayed plumage maturation and
354 delayed reproductive investment in birds. *Biol. Rev.* **87**, 257-274.
- 355 Hiebert, S. M., Stoddard, P. K. & Arcese, P. 1989: Repertorie size, territory
356 acquisition and reproductive success in the song sparrow. *Anim. Behav.* **37**,
357 266-273.
- 358 Immelman, K. 1969: Song development in the zebra finch and other estrildid
359 finches. In: *Bird vocalizations*. (Hinde, R. A., ed). Cambridge University
360 Press, Cambridge. pp. 61-74.
- 361 Järvi, T., Røskaft, E., Bakken, M. & Zumsteg, B. 1987: Evolution of variation in male
362 secondary sexual characteristics. A test of eight hypotheses applied to pied
363 flycatchers. *Behav. Ecol. Sociobiol.* **20**, 161-169.

- 364 Kiefer, S., Sommer, C., Scharff, C., Kipper, S. & Mundry, R. 2009: Tuning towards
365 tomorrow? Common nightingales *Luscinia megarhynchos* change and increase
366 their song repertoires from the first to the second breeding season. *J. Avian*
367 *Biol.* **40**, 231-236.
- 368 Kiefer, S., Spiess, A., Kipper, S., Mundry, R., Sommer, C., Hultsch, H. & Todt, D.
369 2006: First year common nightingales (*Luscinia megarhynchos*) have smaller
370 song type repertoire sizes than older males. *Ethology* **112**, 1217-1224.
- 371 Kipper, S. & Kiefer, S. 2010: Age-related changes in birds' singing styles: on fresh
372 tunes and fading voices? *Adv. Study Behav.* **41.**, 77-118.
- 373 Konishi, M. 1994: An outline of recent advances in birdsong neurobiology. *Brain*
374 *Behav. Evol.* **44**, 279-285.
- 375 Lambrechts, M. & Dhondt, A. A. 1986: Male quality, reproduction, and survival in
376 the great tit (*Parus major*). *Behav. Ecol. Sociobiol.* **19**, 57-63.
- 377 Lampe, H. M. & Espmark, Y. O. 1994: Song structure reflects male quality in pied
378 flycatchers, *Ficedula hypoleuca*. *Anim. Behav.* **47**, 869-876.
- 379 Lampe, H. M. & Sætre, G. P. 1995: Female pied flycatchers prefer males with larger
380 song repertoires. *Proc. R. Soc. Lond. B* **262**, 163-167.
- 381 Lampe, H. M. & Espmark, Y. O. 2003: Mate choice in pied flycatchers *Ficedula*
382 *hypoleuca*: Can females use song to find high-quality males and territories?
383 *Ibis* **145**, E24-E33.
- 384 Lehongre, K., Lenouvel, P., Draganoiu, T. & Del Negro, C. 2006: Long-term effect of
385 isolation rearing conditions on songs of an 'open-ended' song learner species,
386 the canary. *Anim. Behav.* **72**, 1319-1327.
- 387 Lundberg, A. & Alatalo, R. V. 1992: The pied flycatcher. T & A D Poyser, London.

388 Marler, P. 1970a: A comparative approach to vocal learning: song development in
389 white-crowned sparrows. *J. Comp. Physiol. Psych.* **71**, 1-25.

390 Marler, P. 1970b: Birdsong and speech development: could there be parallels? There
391 may be basic rules governing vocal learning to which many species conform,
392 including man. *Am. Sci.* **58**, 669-673.

393 Marler, P. 1990: Song learning: The interface between behaviour and neuroethology.
394 *Phil. Trans. R. Soc. Lond. B* **329**, 109-114.

395 Marler, P. R. & Slabbekoorn, H. 2004: *Nature's Music: The Science of Birdsong*.
396 Academic Press, New York.

397 McGregor, P. K., Krebs, J. R. & Perrins, C. M. 1981: Song repertoires and lifetime
398 reproductive success in the great tit (*Parus major*). *Am. Nat.* **118**, 149-159.

399 Moran, M. D. 2003: Arguments for rejecting the sequential Bonferroni in ecological
400 studies. *Oikos* **102**, 403-405.

401 Nakagawa, S. 2004: A farewell to Bonferroni: the problems of low statistical power
402 and publication bias. *Behav. Ecol.* **15**, 1044-1045.

403 Nicholson, J. S., Buchanan, K. L., Marshall, R. C. & Catchpole, C. K. 2007: Song
404 sharing and repertoire size in the sedge warbler, *Acrocephalus schoenobaenus*:
405 changes within and between years. *Anim. Behav.* **74**, 1585-1592.

406 Nordby, J. C., Campbell, S. E. & Beecher, M. D. 2002: Adult song sparrows do not
407 alter their song repertoires. *Ethology* **108**, 39-50.

408 Nottebohm, F. 1968: Auditory experience and song development in the chaffinch
409 *Fringilla coelebs*. *Ibis* **110**, 549-568.

410 Nowicki, S., Peters, S. & Podos, J. 1998: Song learning, early nutrition and sexual
411 selection in songbirds. *Am. Zool.* **38**, 179-190.

412 Perneger, T. V. 1998: What's wrong with Bonferroni adjustments. *Br. Med. J.* **316**,
413 1236-1238.

414 Poesel, A. & Nelson, D. A. 2012: Delayed song maturation and territorial aggression
415 in a songbird. *Biol. Lett.* **8**, 369-371.

416 Potvin, D. A., Crawford, P. W., MacDougall-Shackleton, S. A. & MacDougall-
417 Shackleton, E. A. 2015: Song repertoire size, not territory location, predicts
418 reproductive success and territory tenure in a migratory songbird. *Can. J. Zool.*
419 **93**, 627-633.

420 Roberts, T. F., Gobes, S. M. H., Murugan, M., Olveczky, B. P. & Mooney, R. 2012:
421 Motor circuits are required to encode a sensory model for imitative learning.
422 *Nat. Neurosci.* **15**, 1454-1459.

423 Rohwer, S., Fretwell, S. D. & Niles, D. M. 1980: Delayed maturation in passerine
424 plumages and the deceptive acquisition of resources. *Am. Nat.* **115**, 400-437.

425 Sætre, G. P., Moum, T., Bures, S., Kral, M., Adamjan, M. & Moreno, J. 1997: A
426 sexually selected character displacement in flycatchers reinforces premating
427 isolation. *Nature* **387**, 589-592.

428 Searcy, W. A. & Yasukawa, K. 1996: Song and female choice. In: *Ecology and*
429 *Evolution of Acoustic Communication in Birds*. (Kroodsma, D. E. & Miller,
430 E. H., eds). Cornell University Press, New York. pp. 454-473.

431 Slagsvold, T. & Sætre, G. P. 1991: Evolution of plumage color in male pied
432 flycatchers (*Ficedula hypoleuca*): Evidence for female mimicry. *Evolution* **45**,
433 910-917.

434 Slater, P. J. B. 1989: Bird song learning - Causes and consequences. *Ethol. Ecol.*
435 *Evol.* **1**, 19-46.

- 436 Spector, D. A. 1994: Definition in biology: The case of "bird song". J. Theor. Biol.
437 **168**, 373-381.
- 438 Thorpe, W. H. 1958: The learning of song patterns by birds, with especial reference to
439 the song of the Chaffinch *Fringilla coelebs*. Ibis **100**, 535-570.
- 440 Vabishchevich, A. P. 2012: Two strategies of between-season changes in the song
441 composition of the pied flycatcher. Ann. Zool. Fenn. **49**, 219-230.
- 442 Vehrencamp, S. L., Hall, M. L., Bohman, E. R., Depeine, C. D. & Dalziell, A. H.
443 2007: Song matching, overlapping, and switching in the banded wren: the
444 sender's perspective. Behav. Ecol. Sociobiol. **18**, 849-859.
- 445
- 446

447 Table 1. Mean \pm SE of song and physical variables studied in the two groups
 448 of first time breeders aged 1- or 2-years old ($N_{\text{Age 1}}=15$; $N_{\text{Age 2}}=11$) with results
 449 from independent sample t-tests ($N=26$) and p-values. Significant results are
 450 shown in bold ($p<0.05$).
 451

	Mean		Independent t-test	
	1-year old	2-years old	t	p
Syllable repertoire size	25.73 \pm 2.67	23.91 \pm 3.13	0.44	0.66
Total N° syllables/song	9.39 \pm 0.33	8.10 \pm 0.35	2.64	0.01
Different syllables/song	4.62 \pm 0.26	4.15 \pm 0.39	1.03	0.31
Sample versatility	0.12 \pm 0.01	0.12 \pm 0.01	0.03	0.97
Song versatility	0.49 \pm 0.02	0.50 \pm 0.03	-0.44	0.66
Song duration (s)	2.00 \pm 0.08	1.78 \pm 0.09	1.80	0.08
Tarsus length (mm)	19.72 \pm 0.12	19.78 \pm 0.12	-0.31	0.76
Body mass (g)	14.27 \pm 0.25	14.11 \pm 0.26	0.4	0.69
Plumage color	4.68 \pm 0.29	3.20 \pm 0.29	3.45	<<0.01

452

453

454 Table 2. Mean \pm SE of song and physical variables measured in the first breeding
 455 season from males that returned a second breeding season (N=11) and from those that
 456 never returned (N=15). The results from independent sample t-tests and p-values
 457 (N=26) are included.

458

	Mean		Independent t-test	
	Returning	Non-returning	t	p
Syllable repertoire size	21.91 \pm 2.21	27.20 \pm 2.99	1,33	0,2
Total N° syllables/song	8.73 \pm 0.32	8.93 \pm 0.41	0,36	0,72
Different syllables/song	4.17 \pm 0.24	4.61 \pm 0.34	0,97	0,34
Sample versatility	0.11 \pm 0.01	0.12 \pm 0.01	0,24	0,81
Song versatility	0.48 \pm 0.02	0.51 \pm 0.02	1,02	0,32
Song duration(s)	1.95 \pm 0.11	1.88 \pm 0.08	-0,53	0,6
Tarsus length (mm)	19.69 \pm 0.16	19.79 \pm 0.10	0.57	0.57
Body mass (g)	14.01 \pm 0.28	14.35 \pm 0.25	0.90	0.38
Plumage color	4.07 \pm 0.47	4.05 \pm 0.29	-0.04	0.97

459

460

461 Table 3. Mean \pm SE of song and physical variables measured in two consecutive
 462 breeding seasons. The results of paired sample t-tests are included. Significant results
 463 are shown in bold ($p < 0.05$). $N=7$ for the song variables and $N=11$ for the physical
 464 measurements.

	Mean		Paired t-test	
	Breeding season 1	Breeding season 2	t	p
Syllable repertoire size	16.05 \pm 2.76	31.29 \pm 3.34	-7.98	<<0.01
Total N° syllables/song	8.79 \pm 0.50	8.78 \pm 0.63	0.01	0.99
Different syllables/song	4.01 \pm 0.36	4.42 \pm 0.41	-1.51	0.18
Sample versatility	0.10 \pm 0.01	0.14 \pm 0.01	-2.51	0.05
Song versatility	0.45 \pm 0.02	0.50 \pm 0.02	-2.84	0.03
Song duration (s)	2.01 \pm 0.16	2.03 \pm 0.19	-0.16	0.88
Tarsus length (mm)	19.69 \pm 0.16	19.73 \pm 0.13	0.25	0.81
Body mass (g)	12.13 \pm 0.13	12.30 \pm 0.19	1.27	0.23
Plumage color	4.07 \pm 0.47	3.47 \pm 0.24	-1.61	0.14

465

466

467 Figure legends

468

469 Fig. 1 Chronogram of the pied flycatcher males included in the study for which we
470 obtained song recordings and physical measurements during their first breeding
471 attempt. The two horizontal lines represent the two patterns of annual presence at the
472 breeding site. In the first case, 15 individuals came back the first year after hatching,
473 when they were 1-year old. For five of these 15 individuals were recorded and
474 measured the following breeding season when they were 2-years old. In the second
475 case, 11 males came back for the first time to the breeding site when they were 2-
476 years old. Among these, two males were recorded and measured the following season
477 when they were 3-years old. We grouped males according to their breeding
478 experience (26 were first time breeders and seven were second time breeders).

479

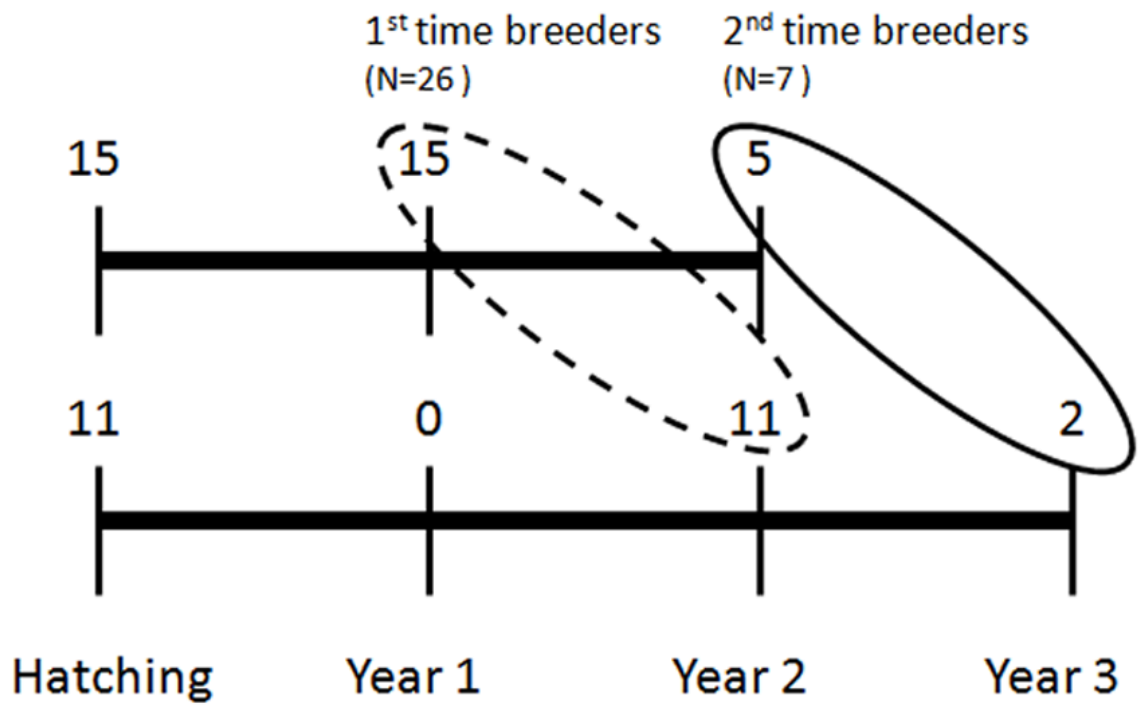
480 Fig. 2. Sonogram of an example of a pied flycatcher song. The numbers on top of
481 the figure indicate different syllable types. For this song, the duration is 2.32 s, the
482 total number of syllables is 10, the total number of different syllables is six, and the
483 song versatility is 0.60.

484

485 Fig. 3 Changes in the repertoire sizes from the first to the second breeding season
486 of seven males of two ages.

487

488



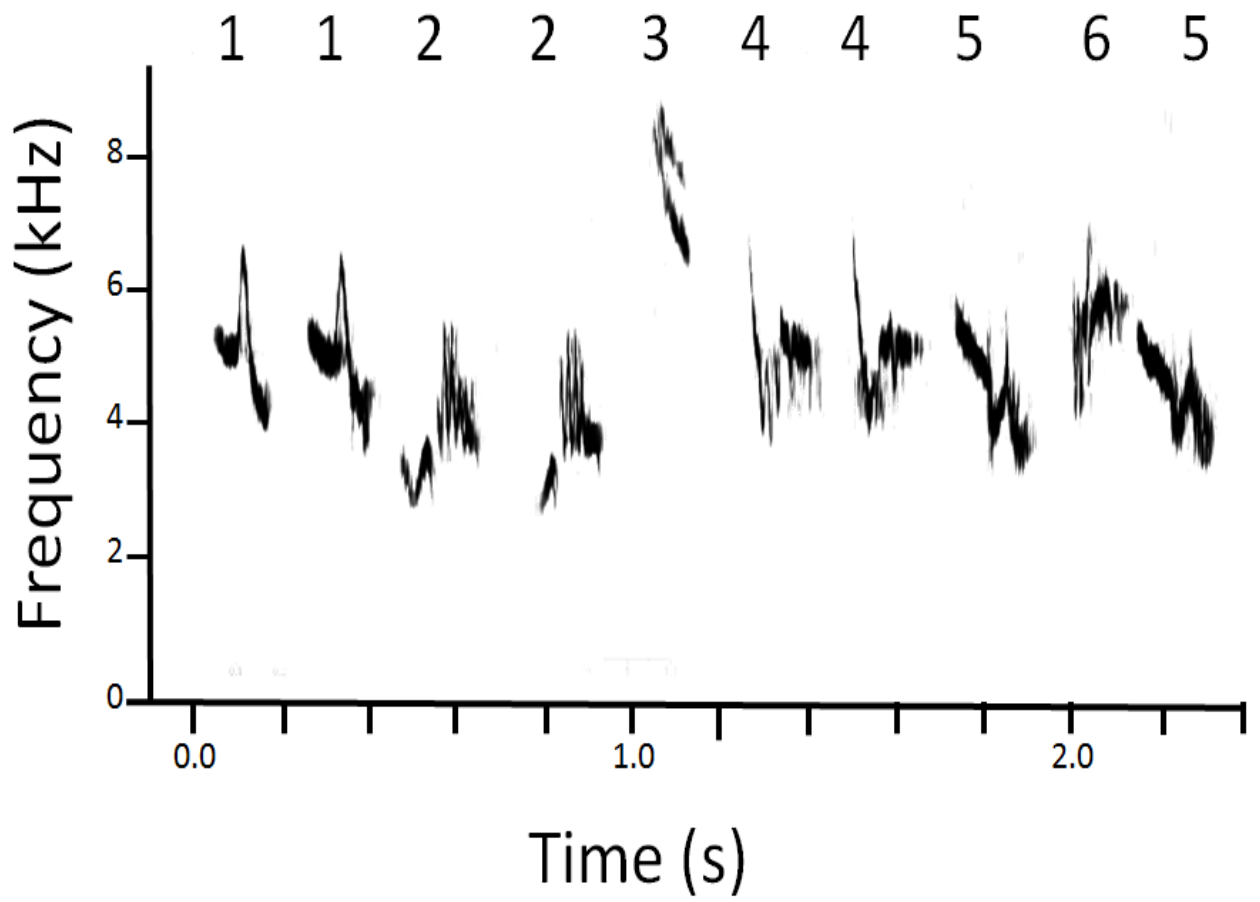
490

491

492 Figure 1

493

494



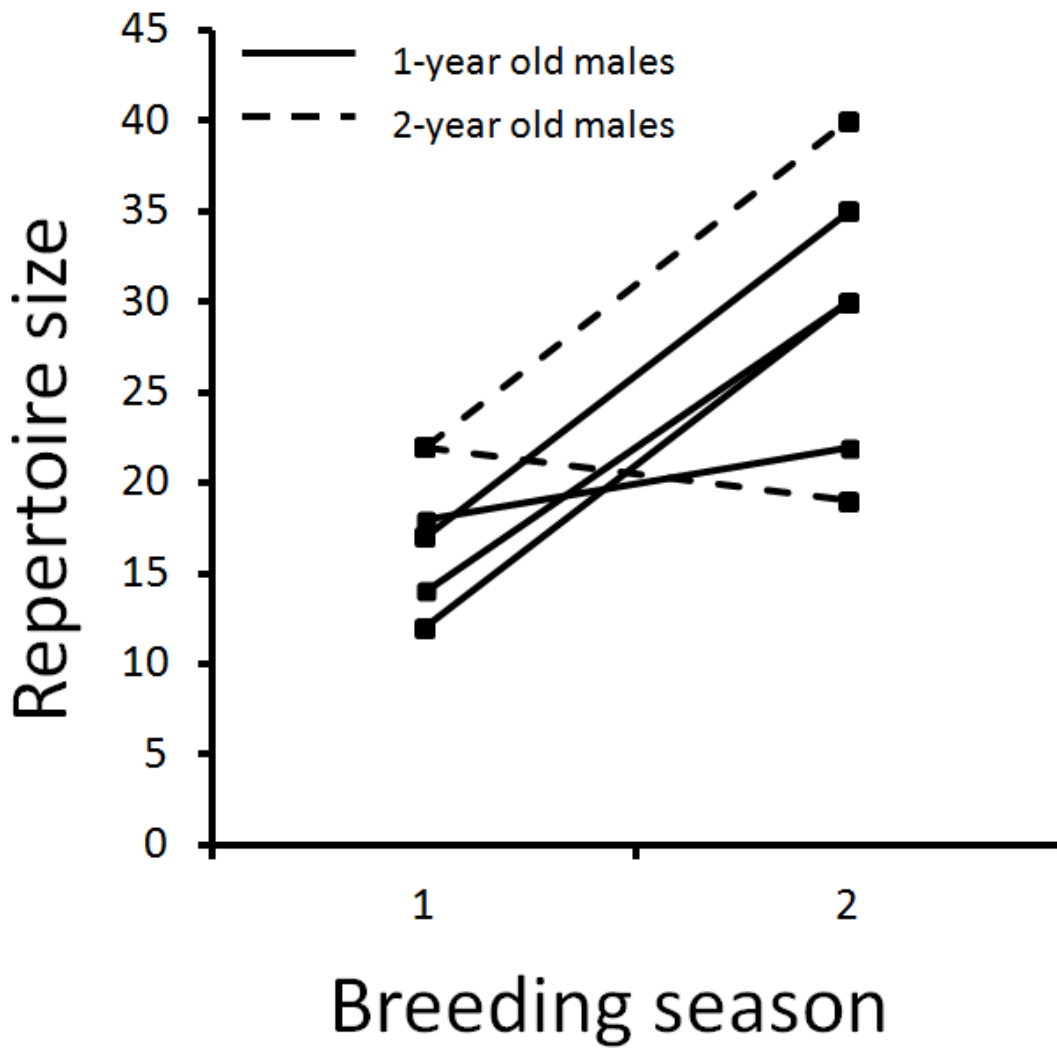
495

496

497 Figure 2

498

499



500

501

502 Figure 3