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

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Abstract

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

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

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

The process of developing the species-specific adult song is highly complex, and involves two phases: memorization and rehearsal (Marler 1970a; Slater 1989; Konishi 1994; Catchpole & Slater 1995; Nowicki et al. 1998). In the memorization phase, song is learned from a tutor (Marler 1970a; Marler & Slabbekoorn 2004). In zebra finches (Taeniopygia guttata) for example, this phase usually takes place during a short period that begins one to two weeks after hatching and lasts for about 30-60 days (Immelmann 1969; Roberts et al. 2012). In the second phase, the rehearsal or motor phase, birds adjust their songs to match what they learned previously. In early stages of the phase, birds sing amorphous songs (subsongs) that develop later on into more variable songs (plastic songs), which finally evolve into stereotyped (crystalized) copies of the model they memorized earlier (Marler 1990; Bolhuis & Gahr 2006). Individuals that do not have a model to imitate produce abnormal songs when they become adults (Thorpe 1958; Nottebohm 1968).
Songbird species vary in the length of these two phases of the learning period (Marler & Slabbekoorn 2004). On the one hand, the age-limited or close-ended learner species, have a learning window limited to the first year of life and are not able to learn new song elements after the crystallization period (Marler 1990), as in the case of song sparrows (*Melospiza melodia*; Nordby et al. 2002) and zebra finches (Böhner 1990). On the other hand, open-ended learners can learn new songs rather continuously throughout life by incorporating new song elements (Marler 1990). They have high vocal plasticity and their song changes with age and often their repertoire size is smaller in yearlings (Kipper & Kiefer 2010), as in nightingales (*Luscinia megarhynchos*; Kiefer et al. 2006) and canaries (*Serinus canaria*; Lehongre et al. 2006).

The existence of smaller repertoires in younger males has been explained by the delayed song maturation hypothesis (Cucco & Malacarne 2000; Poesel & Nelson 2012). Accordingly, younger males would benefit from having a limited song repertoire as this may lead to less competition with older males. A similar phenomenon occurs regarding male plumage color. In this case, delayed plumage maturation refers to clearly distinguishable male plumage features between the 1-year old and adult individuals, thus 1-year old males resemble physically females although they are sexually mature (Rohwer et al. 1980; Hawkins et al. 2012). Furthermore, it has been suggested that the main differences in plumage color maturation can be observed between 1-year old and older males (Cucco & Malacarne 2000). Thus, plumage and songs seem to respond to similar selective pressures, as Cucco and Malacarne (2000) found for the species from which data was available; delayed song maturation was associated with delayed plumage color maturation.
Previous data, thus, provide clear evidence that for different open-ended learner species, age is a determining factor of male song variation (Kipper & Kiefer 2010). However, there are different patterns to when the learning process takes place. There are species which songs change only from year 1 to 2, as can be observed in nightingales (Kiefer et al. 2006; Kipper & Kiefer 2010), banded wrens (Thryothorus pleurostictus, Vehrencamp et al. 2007), collard flycatchers (Garamszegi et al. 2007), and whitethroats (Sylvia communis; Balsby 2000; Balsby & Hansen 2010). In contrast, there are species that change their songs years after, such as barn swallows (Hirundo rustica, Galeotti et al. 2001), sedge warblers (Acrocephalus schoenobaenus, Nicholson et al. 2007), and pied flycatchers (Ficedula hypoleuca, (Lundberg & Alatalo 1992; Espmark & Lampe 1993; Eriksen et al. 2011; Vabishchevich 2012).

Breeding experience may be another relevant factor to explain male song variation in open-ended learners since songs are learned from neighbors during the breeding season (Lundberg & Alatalo 1992; Kiefer et al. 2009; Kipper & Kiefer 2010), but the individual contribution of age and breeding experience is not yet clear. For that reason, in the present study we aimed to assess if known-age male pied flycatchers increase their repertoires as well as other song variables, as they become older or more experienced breeders. In this species, differences in song characteristics across individuals can be highly relevant for female choice. Females are more attracted to males that sing larger and more complex repertoires (Lampe & Sætre 1995) and repertoire size has been suggested to be a sign of territory quality (Lampe & Espmark 2003). In addition, repertoire size correlates with the arrival order, experience, body mass, condition and plumage color (Lampe & Espmark 1994), and darker males are preferred by females (Sætre et al. 1997). Moreover, males with higher song rate pair
earlier, suggesting that the song rate may be interpreted by females as indicative of territory quality and/or male quality (Gottlander 1987).

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

Methods

Songs of pied flycatcher males were recorded before they were mated, during the breeding seasons between 1997 and 2013. The breeding area is a mixed coniferous forest at Sinober in Sørkedalen (59°59’N, 10°38’E, 160-200 m asl) near Oslo (Norway), where wooden nestboxes are found at 30-50 m intervals. The approximate dimensions of the nest boxes were 11 x 13 x 21 cm on the inside, 15 x 17 x 27 cm on the outside, with a 3.5 cm diameter opening and 15 cm height to the opening. The area was monitored every day to check the arrival of the males, which on average, arrive a week before females (Lundberg & Alatalo 1992; Canal et al. 2012). After
recording them, males were captured in the nestbox they defended, and weighted to
the nearest 0.1 g with a Pesola spring balance. Tarsus length was measured with toes
bent from the extreme bending point at the inter-tarsal joint with a sliding caliper to
the nearest 0.5 mm. The plumage color was measured by comparing it with a Drost
color scale (Drost 1936), where I is completely black head and back and VII
completely brown. Males included in this study had been banded as nestlings with
uniquely numbered aluminum rings, but we also gave them two color rings on their
first capture as adults for easier identification if they returned in subsequent years.

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

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

For each male, we analyzed a sample of 25 consecutive songs. The sound files
were analyzed using RAVEN pro version 1.4 (Cornell Laboratory of Ornithology,
Ithaca, NY), with a sample rate of 44100 Hz and 16-bit resolution and a discrete
Fourier Transformation size of 256 together with a sonogram overlap of 50%. From
direct visual inspection of the sonogram we determined the different syllables of each
song (Lundberg & Alatalo 1992). A syllable is a continuous song element or group of elements separated from each other by more than 0.02 s (Fig. 2). If the separation is more than 1 s, it is considered a new song. In total, seven variables were calculated for each individual per breeding season based on variables that have been shown to be important for female choice (Lampe & Espmark 2003).

1- Song duration, to the nearest 0.01 s.
2- Total number of syllables per song.
3- Total number of different syllables per song.
4- Total number of syllables in the whole sample (25 songs).
5- Syllable repertoire size, the total number of different syllables in the whole sample (25 songs).
6- Song versatility. The ratio between 3 and 2: Total number of different syllables per song/Total number of syllables per song.
7- Sample versatility. The ratio between 5 and 4: Syllable repertoire size/Total number of syllables in the whole sample.

Two-tailed Student's t-tests for independent samples were conducted after testing for normality in order to analyze if there were significant differences among the song variables and physical measurements between (i) the 1- and 2-years old first time breeding males and (ii) the males returning a second breeding season versus the non-returning males. Two-tailed paired samples t-tests were used to analyze the differences among song variables and physical measurements between the males recorded in two consecutive breeding seasons. Bonferroni corrections were not applied on significant data because of the controversy about its limitations in the field of ecology and ethology (Perneger 1998; Moran 2003; Nakagawa 2004). Data was
analyzed with SPSS (IBM Analytics), statistical significance was set at \( p < 0.05 \) and values are reported as Mean ± SE.

**Results**

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

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

The song variables of those males that were recorded in two consecutive breeding seasons showed a significant increase between years for those variables associated to complexity, i.e. sample and song versatility as well as repertoire size (Table 3).

Moreover, the latter almost doubled on average from the first to the second year (Fig. 3). Morphology and plumage color did not change between breeding seasons (Table 3).

**Discussion**

Repertoire size has been generally accepted to act as an indicator of male age in open-ended learners (see Kipper & Kiefer 2010 for a review), but our results suggest a different picture. Comparisons of the song variables of 26 known-age male pied
flycatchers banded as nestlings and subsequently recorded at the breeding site in their first breeding season when either 1- or 2-years old, showed no significant effect of age. However, the song characteristics associated with complexity differed between the first and second time males were at the breeding site, and males almost doubled their repertoire in the second season. Thus, our data indicate that for pied flycatchers the males’ breeding experience, instead of their age, is a determinant factor for their repertoire size and other song characteristics revealing song complexity.

Some previous studies analyzing the changes in the songs of 1- and 2-years old pied flycatchers also showed no variation between years (Espmark & Lampe 1993; Eriksen et al. 2011), but these studies presented some limitations as the authors included few 1-year old males (five in Eriksen et al. 2011) or assumed all first time breeders to be 1-year old (Espmark & Lampe 1993). In our study, where we controlled for the breeding experience, we found similarities in song characteristics between males of the two age groups. These results differ however, from what has been found in yearlings of the closely related collared flycatcher (*Ficedula albicollis*), which had smaller repertoires than older males (Garamszegi et al. 2007). A key factor to explain these differences may be the level of the analysis (Kiefer et al. 2009); while we analyzed longitudinal changes, Garamszegi et al. (2007) analyzed cross-sectional changes. In fact, both flycatcher species show an overall positive relationship between repertoire size and age at the cross-sectional, population level (Lundberg & Alatalo 1992; Lampe & Espmark 1994; Garamszegi et al. 2007). Nevertheless, the type of analyses seems not to be enough to explain variation in song development of pied flycatchers. In a population of Russian pied flycatchers, some yearlings showed delayed song maturation, while other yearlings did not, singing indistinguishable from adult males (Vabishchevich 2012).
In our population of pied flycatchers, breeding experience significantly affected the song variables associated with song complexity (repertoire size, sample and song versatilities), as was indicated previously in common nightingales (Kiefer et al. 2009). The biological significance of conveying the breeding experience through the song is justified if some males do not return to the breeding site the first year after hatching, remain in the wintering grounds instead of migrating north as is the case of the pied flycatcher (Lundberg & Alatalo 1992). Independently of why males do not come back, when they do return there would be an impairment between their age and their breeding experience, as their breeding experience will be equivalent to that of younger males. When this is the case, and since females prefer larger repertoires (Lampe & Sætre 1995; Lampe & Espmark 2003), there might be a strong sexual selection for song complexity to be an honest indicator of male breeding experience rather than an exclusively age-dependent trait. A higher complexity in the songs may inform the females that the singer already has the skill to find a good territory and defend it, as males sing to attract females once they are ready to mate (Lundberg & Alatalo 1992). The increased song complexity between the first two breeding seasons implies that males learn new syllables from their neighbors that sing in the breeding area (Lundberg & Alatalo 1992; Eriksen et al. 2011) and not in the winter grounds. Previous studies indicate that pied flycatchers learn after the second breeding season (Eriksen et al. 2011), but it remains unclear how much annual breeding experience continues to modulate song characteristics after the second breeding season. The pattern of song learning seems to be reflected in expected longevity since the long-lived species learn new songs throughout their lives (an exception is the sedge warbler that may only live to be six years old but still learn to new songs each year, Cucco & Malacarne 2000). Both pied flycatcher and barn swallows have maximum
ages of around 15 years, while the nightingale and collared flycatcher may live to be half that age (Cucco & Malacarne 2000).

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

The pied flycatcher shows delayed plumage maturation (Järvi et al. 1987), and in agreement, we also found a significant difference in plumage color between 1-year old and 2-years old males, which may reduce aggression from other males but increase aggression from females (Slagsvold & Sætre 1991). In this context, increase in the number of syllables per song may be a good strategy for the 1-year old males to compensate for their plumage color, to make the song more attractive to females.
However, since the most important variables for attracting females are related to song complexity (repertoire size, song and sample versatility; Lampe & Sætre 1995), and these were similar for 1- and 2-years old males, it is unlikely that having more syllables per song can counter the age effect. Alternatively, 1-year old males could sing more syllables to increase the efficiency of territory defense, as was suggested to occur for the song rate in collared flycatchers, where yearlings sing at higher rates and respond more aggressively towards intruders than older males do (Garamszegi et al. 2006; Garamszegi et al. 2007). In the case of pied flycatcher, this is also an unlikely hypothesis as males rarely evict other males, and song is primarily used in female attraction (Lundberg & Alatalo 1992). It is more probable that the high number of syllables per song sang at an early age may be equivalent to a “plastic phase” in the motor phase of song learning, when males have more syllables in their songs and rehearse the syllables that later on will constitute their repertoire (Marler 1970b).

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

Acknowledgements

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


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

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>Independent t-test</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1-year old</td>
<td>2-years old</td>
<td>t</td>
</tr>
<tr>
<td>Syllable repertoire size</td>
<td>25.73±2.67</td>
<td>23.91±3.13</td>
<td>0.44</td>
</tr>
<tr>
<td>Total N° syllables/song</td>
<td>9.39±0.33</td>
<td>8.10±0.35</td>
<td>2.64</td>
</tr>
<tr>
<td>Different syllables/song</td>
<td>4.62±0.26</td>
<td>4.15±0.39</td>
<td>1.03</td>
</tr>
<tr>
<td>Sample versatility</td>
<td>0.12±0.01</td>
<td>0.12±0.01</td>
<td>0.03</td>
</tr>
<tr>
<td>Song versatility</td>
<td>0.49±0.02</td>
<td>0.50±0.03</td>
<td>-0.44</td>
</tr>
<tr>
<td>Song duration (s)</td>
<td>2.00±0.08</td>
<td>1.78±0.09</td>
<td>1.80</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>19.72±0.12</td>
<td>19.78±0.12</td>
<td>-0.31</td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>14.27±0.25</td>
<td>14.11±0.26</td>
<td>0.4</td>
</tr>
<tr>
<td>Plumage color</td>
<td>4.68±0.29</td>
<td>3.20±0.29</td>
<td>3.45</td>
</tr>
</tbody>
</table>
Table 2. Mean ± SE of song and physical variables measured in the first breeding season from males that returned a second breeding season (N=11) and from those that never returned (N=15). The results from independent sample t-tests and p-values (N=26) are included.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Returning</th>
<th>Non-returning</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Syllable repertoire size</td>
<td>21.91±2.21</td>
<td>27.20±2.99</td>
<td>1.33</td>
<td>0.2</td>
</tr>
<tr>
<td>Total N° syllables/song</td>
<td>8.73±0.32</td>
<td>8.93±0.41</td>
<td>0.36</td>
<td>0.72</td>
</tr>
<tr>
<td>Different syllables/song</td>
<td>4.17±0.24</td>
<td>4.61±0.34</td>
<td>0.97</td>
<td>0.34</td>
</tr>
<tr>
<td>Sample versatility</td>
<td>0.11±0.01</td>
<td>0.12±0.01</td>
<td>0.24</td>
<td>0.81</td>
</tr>
<tr>
<td>Song versatility</td>
<td>0.48±0.02</td>
<td>0.51±0.02</td>
<td>1.02</td>
<td>0.32</td>
</tr>
<tr>
<td>Song duration(s)</td>
<td>1.95±0.11</td>
<td>1.88±0.08</td>
<td>-0.53</td>
<td>0.6</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>19.69±0.16</td>
<td>19.79±0.10</td>
<td>0.57</td>
<td>0.57</td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>14.01±0.28</td>
<td>14.35±0.25</td>
<td>0.90</td>
<td>0.38</td>
</tr>
<tr>
<td>Plumage color</td>
<td>4.07±0.47</td>
<td>4.05±0.29</td>
<td>-0.04</td>
<td>0.97</td>
</tr>
</tbody>
</table>
Table 3. Mean ± SE of song and physical variables measured in two consecutive breeding seasons. The results of paired sample t-tests are included. Significant results are shown in bold (p<0.05). N=7 for the song variables and N=11 for the physical measurements.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Breeding season 1</th>
<th>Breeding season 2</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Syllable repertoire size</td>
<td>16.05±2.76</td>
<td>31.29±3.34</td>
<td>-7.98</td>
<td>&lt;&lt;0.01</td>
</tr>
<tr>
<td>Total N° syllables/song</td>
<td>8.79±0.50</td>
<td>8.78±0.63</td>
<td>0.01</td>
<td>0.99</td>
</tr>
<tr>
<td>Different syllables/song</td>
<td>4.01±0.36</td>
<td>4.42±0.41</td>
<td>-1.51</td>
<td>0.18</td>
</tr>
<tr>
<td>Sample versatility</td>
<td>0.10±0.01</td>
<td>0.14±0.01</td>
<td>-2.51</td>
<td>0.05</td>
</tr>
<tr>
<td>Song versatility</td>
<td>0.45±0.02</td>
<td>0.50±0.02</td>
<td>-2.84</td>
<td>0.03</td>
</tr>
<tr>
<td>Song duration (s)</td>
<td>2.01±0.16</td>
<td>2.03±0.19</td>
<td>-0.16</td>
<td>0.88</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>19.69±0.16</td>
<td>19.73±0.13</td>
<td>0.25</td>
<td>0.81</td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>12.13±0.13</td>
<td>12.30±0.19</td>
<td>1.27</td>
<td>0.23</td>
</tr>
<tr>
<td>Plumage color</td>
<td>4.07±0.47</td>
<td>3.47±0.24</td>
<td>-1.61</td>
<td>0.14</td>
</tr>
</tbody>
</table>
Fig. 1 Chronogram of the pied flycatcher males included in the study for which we obtained song recordings and physical measurements during their first breeding attempt. The two horizontal lines represent the two patterns of annual presence at the breeding site. In the first case, 15 individuals came back the first year after hatching, when they were 1-year old. For five of these 15 individuals were recorded and measured the following breeding season when they were 2-years old. In the second case, 11 males came back for the first time to the breeding site when they were 2-years old. Among these, two males were recorded and measured the following season when they were 3-years old. We grouped males according to their breeding experience (26 were first time breeders and seven were second time breeders).

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

Fig. 3 Changes in the repertoire sizes from the first to the second breeding season of seven males of two ages.
Figure 1
Figure 2
Figure 3