The role of arrival time to the breeding grounds in the song development of juvenile pied flycatchers

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Abstract

Few studies on song learning has been conducted in the field. Male pied flycatchers (*Ficedula hypoleuca*) seem to learn song syllables in the breeding grounds. Adult males arrive first to the breeding grounds and sing more complex songs until they have paired. Early arriving juveniles may have more opportunities to learn new syllables from adult neighbours and develop more complex songs than later arriving juveniles. However, results suggest that arrival time is not important in song complexity development, but that males develop greater song complexity (repertoire size and song versatility) regardless as they age.

Introduction

Males are the primary singers of most oscine species, wherein songs are involved in territorial defence against rival males and/or for female attraction (Catchpole and Slater 2008). In the case of mate attraction, evidence from different species indicate that the characteristics of male song may reflect male quality that can affect female choice (Catchpole and Slater 2008; Searcy and Andersson 1986, but see Byers and Kroodsma 2009). However, a meta-study on song complexity revealed that male song characteristics have a weak effect on breeding success (Soma and Garamszegi 2011).

The singing behaviour of oscines is innate, but the content of the song has to be learned (Kroodsma 1982). Song repertoire size (e.g. the number of different song types or syllables in an individual's song) correlates with the mode of learning (open-ended or closed-ended learning, Nottebohm 1984), with open-ended learners having larger song repertoires (Creanza et al. 2016). In the case of the open-ended learners, they are able to continuously learn new syllables and thus change and/or add to their song repertoire as adults and increase their song complexity as observed in most well-studied open-ended learners (Brenowitz and Beecher 2005; Garamszegi et al. 2007; and extensively reviewed in Kipper & Kiefer 2010 for repertoire changes with age). Such is the case for the pied flycatcher (*Ficedula hypoleuca*), known to sing complex songs (Lundberg and Alatalo 1992; Lampe and Espmark 1994). Males learn syllables from conspecifics and heterospecifics in the breeding area (Eriksen et al. 2009; Eriksen et al. 2011), and in general, males increase their song repertoire and complexity as they gain breeding experience and grow older (Espmark and Lampe 1993; Motes-Rodrigo et al. 2017). New evidence indicates that nestlings learn from their fathers in the nest, since sons tend to share more syllables with their fathers than with their fathers' neighbours in their first breeding season (Labra and Lampe 2018). This is probably a consequence of those occasions when fathers sing before entering the nest box to feed the nestlings and it suggests that males begin to develop their song at the earliest opportunity (see also Wheatcroft & Qvarnström 2017).

Pied flycatchers are migratory birds that winter in West Africa south of the Sahel and migrate north to Europe to breed (Lundberg and Alatalo 1992; Ouwehand et al. 2016). In general, the arrival time of male pied flycatchers to spring breeding grounds vary, but older males tend to arrive earlier than juveniles and females (Cadahia et al. 2017; Lundberg and Alatalo 1992). More males sing at the beginning of the breeding season as they are unmated;

once they have paired, males stop their singing activity (Espmark and Lampe 1993). Furthermore, earlier arriving males sing more complex songs than those of late arriving males (Lampe and Espmark 1994), meaning that juveniles will not only be exposed to more singing males, but also to larger repertoires in comparison to males that arrive later in the breeding season. Therefore, early arriving males may have more learning opportunities. If so, it is expected that in the following year, early arriving juveniles may sing songs that are more complex than those of late arriving individuals. To test if arrival time modulates the song complexity of juveniles, we compared the song characteristics of one-year old individuals that arrived early or late to the breeding ground with their songs when they were two-years old. We predict that individuals that arrived earlier as one-year old males will have a bigger increase in song complexity in the following year compared to the late arriving males.

Materials and Methods

The pied flycatcher population studied was from the woodland area of Sinober in Sørkedalen (59°59'N, 10°38'E, 150-200m asl) near Oslo, Norway. Around 225-275 nest boxes, approximately 11x13x21cm on the inside and 15x17x27cm on the outside with a 3.5cm opening diameter and 15cm opening height, were set up at 50m intervals in the ca. 72 ha area. The study area was monitored daily, with the exception of very rainy days when male flycatchers were unlikely to be singing (pers. obs.). Although data collection for the field season differed between years, monitoring began in late April and ended in early July for most years.

We analyzed male pied flycatcher songs recorded during the breeding seasons from 1995 up to and including 2017. The sample size for song analysis was 20 males captured for the first time as juveniles (one year old), and that returned the next year to be recorded again when two years old. Males were recorded on the arrival day or as soon as possible (+1 or 2 days). Thereafter, males were captured and identified, measured, and weighed. New males were banded with a unique numbered aluminium ring and two different coloured rings. Males were aged based on the feathers of their wings (Svensson 1992) to determine if they were juveniles or adults.

From 2007-2017, we recorded songs using Sound Devices 702 digital recorder with parabolic microphones (Telinga Microphones, Sweden). Older recordings were obtained using Sony cassette recorders (TC-D5PROII) which were later digitalized. Recordings were obtained

between 07:30-13:00, depending on the activity of the day. Only males with at least 25 consecutive strophes were analyzed as males typically begin to plateau in the number of syllables sung by 25 strophes (Eriksen et al. 2011). Strophes are defined as a group of syllables that are separated from another group of syllables by at least 1 second (Fig. 1). Syllables are defined as continuous elements or groups of elements separated by at least 0.02s from other syllables (Fig. 1; Lundberg and Alatalo 1992). If a recording had more than 25 strophes, the clearest 25 strophes were analyzed (i.e. no overlap of vocalization with other birds, little background noise).

Song analyses were done using RAVEN 1.5 Software (Cornell Laboratory of Ornithology, Ithaca, NY) with sample rate of 44100 Hz and 16-bit resolution and a discrete Fourier Transformation size of 256 together with a sonogram overlap of 50%. A strophe was included in the analysis if it consisted of at least three syllables. Song variables (characteristics) that were assessed for each male were defined as (for reference see also Lampe and Espmark 2003; Motes-Rodrigo et al. 2017):

- 1) Repertoire size: the total number of different syllables in the individual's song (i.e. 25 strophes).
- 2) Strophe versatility: the ratio of the average number of different syllables in a strophe to the average total number of syllables in a strophe.
- 3) Song versatility: the ratio of repertoire size to the total number of syllables in the song.
- 4) Average strophe duration (s): the mean length (time) of the 25 strophes analyzed.

The juvenile males were split between early and late arrivals amongst the male population of the year when they were first recorded (as one year old). Since the analyzed songs were collected in different years, to standardize arrival dates of early and late arriving males, we ranked juveniles considering: 1) when the first juvenile arrived (male juvenile population), and 2) when the first male arrived from the whole male population (whole male population). Afterwards, the median arrival date of each year was calculated; males arriving before the median date of either the juvenile male or whole male population were considered early and males arriving after the median date were considered late. Because breeding experience influence song complexity (Motes-Rodrigo et al. 2017), we compared the proportion of experienced males in the early vs late group. Mean proportion ($\pm$ SD) of experienced males was 0.50 ± 0.11 (early group) vs 0.27 ± 0.09 (late group), i.e. there were significantly more experienced

males in the early group (one-way ANOVA, $F=33.78$, $p<0.0001$). Thus, our early group should have a higher probability of hearing more complex song.

The distribution of data was tested using the Shapiro-Wilk test and all the data was normally distributed. The effect of the arrival time (early vs. late), the age of the male (one-year old vs. two-years old) and their interaction upon the four song variables were analysed using two-way ANOVAs with repeated measures (age). Analyses was conducted on both arrival time based on juvenile population and whole male population. Since both analyses showed the same trends, we only present and discuss data considering the whole male population. The significance α -levels was $p<0.05$.

Results

For the four song variables studied, the only effect found was of the age on repertoire size and song versatility (Table 1). Regardless of the males' arrival time to the breeding grounds, there was an effect of age; males had an increase in repertoire size and song versatility from one-year old to two-years old (Fig. 2).

Discussion

This study attempted to contribute to the understanding of how pied flycatchers develop their songs, specifically testing the role of the arrival time to the breeding areas and the acquisition of song complexity by juveniles. We hypothesized that song complexity development would be influenced by the arrival time, as early arriving juvenile males will be exposed to more males singing, with more complex songs (Espmark and Lampe 1993; Lampe and Espmark 1994). If so, early arriving males would have a more complex song than late arriving males in the following year. However, the only factor that affected significantly the song complexity development was age, with an increase in repertoire size and song versatility of males from one-year old to two-years old.

There are two non-mutually exclusive hypotheses to explain why arrival time does not modulate song complexity development. The first one is that males are learning syllables during stopovers sites while they are migrating to the spring breeding grounds, and late arriving males may compensate for what they did not hear at the breeding grounds by learning what they hear at the stopover sites. In the case of the white-crowned sparrow (*Zonotrichia leucophrys*), juveniles

have been observed to have learnt some songs during migration (Baptista and Morton 1988). In fact, learning at the stopover sites may explain why pied flycatchers from Denmark have similar syllables as populations found in Norway (Lampe et al. 2007).

The second hypothesis is that males are learning from dawn song, not measured in our study, which occurs in pied flycatchers even after mating (Gottlander 1987; Vabishchevich 2011). Vabishchevich (2011) found that mated males that participated in dawn singing had higher song versatility and song rates, and these males were singing more syllables. It has been proposed that dawn singing may function to attract females for extra pair copulations (Gil and Gahr 2002; Vabishchevich 2011). In the closely related species, collared flycatcher (*Ficedula albicollis*), dawn singing is thought to help males attract new females or re-mate if they have lost a female during the breeding season (Pärt 1991). Therefore, these are syllables that juveniles may learn and incorporate into their own songs. Under this context, it does not matter when the juveniles arrive at spring breeding grounds because there are enough opportunities to learn. Moreover, it is possible that pied flycatcher juveniles will be able to learn new syllables even within a short exposure (i.e. the few hours of dawn singing), such as nightingales (*Luscinia megarhynchos*), which can learn new syllables with 10-30 repetitions (Hultsch and Todt 1992).

In summary, our long-term study shows that arrival time to the breeding area does not modulate the development of song complexity or song duration in juvenile males of pied flycatchers, and only age affects some of the song complexity variables, i.e. males have simpler songs when they are one-year old independent of their arrival time. This is reflected in both repertoire size and song versatility and agrees with previous studies (Espmark and Lampe 1993; Motes-Rodrigo et al. 2017).

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Tables

Table 1. Results of the two-way ANOVA with repeated measures to determine the effect of arrival time (early vs. late arrivals based on arrival time of one-year old males), age (one- vs. two-years old), and their interaction upon four song variables. The arrival time of juveniles was categorized considering the whole male population. There were six individuals categorized as early arriving males and 14 individuals that were categorized as late arriving males, total n=20. Values shown are degree of freedom (df) the F-statistics (p-value). Bold font indicates $p < 0.001$.

Song Variable	Factor	df	F	p
Repertoire Size	Arrival	1	0.207	0.654
	Age	1	16.42	<0.001
	Age*Arrival	1	0.000	0.980
Strophe Versatility	Arrival	1	0.001	0.973
	Age	1	0.591	0.452
	Age *Arrival	1	0.532	0.475
Song Versatility	Arrival	1	1.660	0.214
	Age	1	26.37	<0.001
	Age *Arrival	1	0.014	0.908
Average Strophe Duration	Arrival	1	2.380	0.140
	Age	1	0.176	0.680
	Age *Arrival	1	0.303	0.589

Figure Legends

Figure 1. A sonogram example of a pied flycatcher song strophe and song (represented as two song strophes). The numbers at the top indicate syllable types. The first strophe contains nine syllables with two different syllable types and strophe duration is 1.848s; the second strophe contains eight syllables with three different syllables and strophe duration is 2.171s; the repertoire size is five. The first strophe has a strophe versatility of 0.222; the second strophe has a strophe versatility of 0.375; the song versatility is 0.294. The average strophe duration is 2.010s.

Figure 2. The mean ($\pm$ SE; $n=20$) of the measured song variables of early and late arriving males (arrival time is based on the one-year old males), as one-year old and two-years old. Grey boxes represent early arriving males, and white boxes represent late arriving males. The arrival time of juveniles was categorized considering the whole male population each year. There were six individuals categorized as early arriving males and 14 individuals that were categorized as late arriving males. The mean of a) repertoire size, b) strophe versatility, c) song versatility, and d) average strophe duration (s) is shown on the y-axis and the age is labelled on the x-axis.

*indicates a significant difference $p<0.05$.

Fig. 1

Fig. 2

1

2