Learning of song in the Pied Flycatcher (*Ficedula hypoleuca*)
- A field study

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Abstract

A population of pied flycatchers was studied to examine learning of song syllables within a single breeding season. Males were separated into neighbor groups based on geographical location and access to experienced, potential tutors. A control group containing males which were not neighbors, and which were without access to an experienced tutor, was used to evaluate the results from the other three groups. Non-parametric statistical methods were used to test the associations and correlations of the observed data. One of the three neighbor groups showed a significant amount of repertoire sharing between the males of the group, sharing more song syllables within the group than with the population as a whole, and another group showed a significant correlation between time of recording and repertoire sharing between males. The hypothesis that inexperienced males learned from experienced tutors was not supported by the observed data, nor was the hypothesis that there was an effect of time between recordings of different males on observed song syllable sharing. A difference in song learning between inexperienced adults and juveniles was found, though it was contrary to the prediction that juveniles would learn more than the adults. The control group was not significantly different from the other groups, though this may be due to confounding variables. Inexperienced adults had a higher coefficient of repertoire sharing with experienced males than did the juveniles. Older males shared more song syllables with the population, and experienced males shared the most song syllables with the population. The only clear example of song syllable learning from experienced tutors was found in inexperienced adults. The inexperienced adults shared nearly equal amounts of song syllables with both their tutors, which was something not found in juveniles. A longitudinal study may be necessary to fully chart the learning of song among pied flycatchers.

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Acknowledgements

With a pied flycatcher singing outside my window as I put the finishing touches on my master thesis, it feels like only yesterday that I was out in the field, recording pied flycatcher song and being asked by random passers-by if I were trying to locate large herbivores in the area. I suppose I may have looked the part to the uninitiated, carrying a large parabolic microphone as I was. Fieldwork was a fantastic experience, and being able to work with such wonderful people only made it better. Even on the day when it snowed sideways nothing could diminish the pure enjoyment of being out in the field.

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Introduction

Most animals develop normal species-typical vocal signals without having learned them from an external source. Only three mammalian groups (including humans) and three avian groups (including the oscine passerines, or songbirds) have been found to be capable of vocal learning so far (Beecher 2010).

There are interesting similarities between vocal learning in songbirds and language learning in humans. The similarities include a sensitive period for learning that begins soon after birth or hatching, vocalization practice, and the need for a social context around the learning process (Beecher 2010).

The auditory template model of song development suggests that young birds are hatched with a basic template that helps them to identify their own species' song during their sensitive period for learning. This model has been modified in various ways since its development, but remains the prevalent model of song learning (Catchpole and Slater 2008; Beecher 2010). The exact pattern of song learning differs between species, however, making it difficult to come to general conclusions about how song is learned (Beecher and Brenowitz 2005).

The sensitive learning period varies, with some bird species having a short sensitive period in the first few months of their life, to some learning for the entire first year, to species which can continue to learn throughout their lifetime. These last species, which can add songs to their song repertoires after their first year of existence, are called open-ended learners, while the ones who do not learn beyond their first year are called closed-ended or age-limited learners (Beecher 2010). It is important to distinguish between an open-ended learner and a species in which juvenile individuals memorize far greater repertoires during their sensitive period than they use at any given time as adults. Such an individual might still present a different repertoire from one year to another, but the repertoire would have been learned during the short juvenile sensitive phase and not throughout subsequent years (Catchpole and Slater 2008). Recent evidence suggests that there is a continuum rather than a boundary between closed and open-ended learning, such that the two differ in the degree of plasticity in adult song rather than in the presence or absence of plasticity (Brenowitz and Beecher 2005).

Kipper and Kiefer (2010) reviewed studies of age-related changes in singing across years, searching for general patterns of such change. Repertoire size was smaller in yearlings for most of the studies reviewed, and the increase in repertoire size was greater between the first and second year, than between any subsequent years. The review showed that vocal plasticity exists and that song changes with age, but that there is no consistent pattern of change (Kipper and Kiefer 2010).

Eens (1997) suggested that repertoire size may be an honest signal due to its significant correlation with age, condition and competitive ability in the male European starling. This is supported by several studies showing a significant increase in song repertoire between the first and second year of song expression in a male, where young, first-year males generally have or display smaller repertoires than their older conspecifics (Lampe and Espmark 1994; Gil et al. 2001; Kiefer et al. 2006; Nicholson et al. 2007; Kiefer et al. 2009; Balsby and Hansen 2010) but see Forstmeier et al. (2006) for a contrast in learning strategies among two geographically separate populations of great reed warbler *Acrocephalus arundinaceus*.

Song repertoire size has also been shown to be correlated with measures of male quality in the common nightingales *Luscinia megarhynchos* (Kipper et al. 2006) and yellow-breasted chats *Icteria virens* (Dussourd and Ritchison 2003), male fitness in song sparrows *Melospiza melodia* (Reid et al. 2004; Reid et al. 2005) and the European starling *Sturnus vulgaris* (Eens 1997), and may signal better survival in great tit *Parus major* males (Rivera-Gutierrez et al. 2010). The complexity of a male's song can gives listeners information about his condition (Nowicki et al. 2000; Leitão et al. 2006), his learning ability (Boogert et al. 2008), and his age (Gil et al. 2001) from increased singing proficiency or from having expanded his repertoire beyond that of a juvenile or young adult (Catchpole and Slater 2008).

A review by Byers and Kroodsma (2009) evaluated 47 papers reporting on studies of the relationship between song repertoire size and female mate choice, finding insufficient evidence to conclude that the relationship was significant. Instead, they suggested that song repertoires may have evolved for the purpose of allowing social interactions based on vocal communication using a wide range of messages. Selection for increasingly complex social interactions would favor larger repertoire sizes, and it could be that songbirds are particularly susceptible to such a selection response due to their learning-based system of song development (Byers and Kroodsma 2009).

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Social context is important in song learning, and the lack of such context may skew results in lab experiments on song learning using playback tutors. Field studies showed that birds learned more readily from live tutors than tape-recorded song and that estimates of a species' sensitive period for learning based on lab studies might be wrong (Beecher 2010). Fieldwork has its own set of problems, however, lacking the experimental control of a lab study, and documenting the full song repertoires to ascertain whether a species is a closed or open ended learner is very labor-intensive (Rivera-Gutierrez et al. 2011).

There are two general ways social factors can influence song learning. Young birds may observe interactions between potential song tutors (so-called "eavesdropping") and select tutors or songs based on differences among the observed adults, perhaps retaining songs of higher-status birds, or direct interaction between the young bird and its tutor(s) may affect the learning of song (Beecher and Burt 2004). A lab study on eavesdropping in young song sparrows in which the subjects were exposed to two kinds of adult tutors, one interacting with the subjects directly and another interacting with a different young male, showed that while the subjects learned songs from both tutor models they learned the most from the overheard interaction rather than the direct interaction. Due to the experimental setup it cannot be extrapolated to field conditions, but one implication of the study is that overheard interactions may be more effective because they are less threatening (Beecher et al. 2007). Since replying with the same or similar song type during countersinging can be considered a threat (Beecher and Brenowitz 2005) the tutor may perceive the student as competition, and there may be problems due to conflicting interests as well (Beecher et al. 2007).

The pied flycatcher (*Ficedula hypoleuca*) is the focus of this study; a small, migratory passerine bird which breeds in forested areas of the Palaearctic region, arriving at its breeding grounds during spring. The male sings until a mate has been acquired, after which singing activity is greatly reduced (Lundberg and Alatalo 1992).

In a study that introduced foreign song syllables to a wild population of pied flycatcher males from playback stimuli Eriksen et al. (2011) found that the males were able to include the newly learned song syllables in their song in the same breeding season, showing that the pied flycatcher is among the open-ended learners. That the pied flycatcher might be an open-ended learner was something which had been proposed in the past by Espmark and Lampe (1993), who found the repertoires of pied flycatcher males to change and increase between breeding seasons.

Female pied flycatchers choose multiple traits in their males, one of which is song versatility (Sirkiä and Laaksonen 2009), and they are able to distinguish between the songs of their mate, their neighbours and strangers, perhaps both to detect intruders and to prevent their mate from establishing a second brood with another female (Lampe and Slagsvold 1998). Song repertoire size was found to correlate with traits signifying male quality in the pied flycatcher (Lampe and Espmark 1994), and females showed preference for large repertoires in an experiment where territory quality was removed from the equation (Lampe and Saetre 1995). Another experiment by Lampe and Espmark (2003) showed that pied flycatcher males with larger song repertoires and more complex song had a greater chance of becoming paired, were in better condition, and also defended the most popular territories in the wild.

The aim of this study was to examine learning of song among pied flycatchers in the field during a single breeding season, looking at whether experienced males, who were present at the study site the previous year and as such are considered familiar with it, function as tutors for inexperienced males. "Inexperienced males" refers in this case both to juveniles entering their first breeding season and to adult males who are unfamiliar with the study site. By comparing groups of males with access to tutors with a group without tutors, I wanted to investigate the following hypotheses:

(1) Inexperienced males learn from experienced tutors.

    i. The proportion of shared song syllables with the group should be higher than with the population.

    ii. The coefficient of sharing (RS) should be greater within a group than for the whole population.

    iii. Inexperienced males should have higher RS with experienced tutors in their group than with experienced tutors outside of the group and with other males inside their group.

(2) There is a difference in song learning between inexperienced adults and juveniles

    i. Juveniles should have higher RS with experienced tutors than inexperienced adults

(3) There is an effect of time between recordings of different males on observed song syllable sharing.

    i. Males recorded later should resemble tutor more than males recorded close to the time the tutor was recorded.

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Methods

Study site

The study area is a mixed coniferous forest, connected to and interspersed with some farmland, at Sørkedalen (59°59'N, 10°38'E) on the outskirts of Oslo, Norway. A total of 257 nest boxes have been placed in the study area, approximately 50m apart, for use by pied flycatchers and other species with whom it competes for nesting space. The study population has been the focus of several research projects over the years, including several that are still ongoing.

Study subjects

Fieldwork began April 26th in anticipation of the soon to be arriving pied flycatcher males. The study area was monitored during the active singing period between 0700 and 1500 for arriving males except for days of heavy rainfall where song would not occur. Dawn song was not recorded. Once a male was encountered, his song was recorded and the male subsequently captured for individual identification by color rings and the breast feathers marked with high-visibility red marker for easy visual confirmation, in order to avoid re-recording and recapturing an already recorded male. The bright red markings, which faded away before the end of the breeding season, had no discernible effect on the male's reproductive success (pers. obs.) nor were there previous indications that this should be the case (Lampe, pers. comm.). The first recording was made on May 5th and the last recording on June 21st of 2010. Each male was only recorded once.

Age of the males was assessed by examining their molt patterns and feather quality, particularly of the outer greater coverts. Young birds retain their original outer greater coverts while adults replace these during the summer molt, this results in color differences that can be used to assess their age (Lundberg and Alatalo 1992). The males which had been observed at the study site the previous year were categorized as Experienced while the males that were new to the study site were categorized as Inexperienced, regardless of whether these inexperienced males were juveniles (1 year old) or adults (2 years old or older). Age was uncertain in five of the inexperienced males, but they were assigned to the age group they were most likely to belong to on the basis of the age assessment that was done in the field.

Of the 18 males recorded in this study, 6 were categorized as experienced. Of the inexperienced males, 9 were juveniles and 3 were adults.

Males were divided into four different groups (North 1 (NG1), North 2 (NG2), South (SG) and Inexperienced-only (IG)) depending on their geographical location at the time of song recording and access to an experienced neighbor as potential tutor.

Neighbors were defined as males recorded at nest boxes within a 100m radius of where the male had been recorded. Three of the four groups contained two experienced males each, in addition to all inexperienced males found within 100m of their recorded nest box. Each group was geographically separate from the other three. NG1 had three inexperienced males, NG2 had one inexperienced male and SG had four inexperienced males. The fourth group contained four inexperienced males without direct access to an experienced neighbor, and the four males were from different parts of the study area. This group was intended to function as a control, lacking both the experienced neighbors and the close geographical association of the other three groups.

Song recording and syllable cataloguing

Songs were recorded using a Telinga Pro6 parabolic microphone and a Sound Devices 702 recorder. Over the course of the breeding season up to four units of recording equipment were in use at any given day in order to be able to cover the study area. Recordings were made in lossless Wave format. The songs were recorded with a sample rate of at least 44100Hz and 16-bit encoding. For each male the recording began at a random point in their daily singing before pairing. Five of the adult males (three experienced, two inexperienced) were mated before recording, and they were all recorded singing at a secondary nest box.

For each recording 25 consecutive song phrases were analyzed and the song syllables used in these phrases were catalogued. A song phrase is defined here as a sequence of two or more song syllables, separated from other sequences by an interval of varying length but at least 1s long. Song syllables are the basic song units, and a male's song repertoire is made up by all the song syllables he sings (Espmark and Lampe 1993). An example of a song phrase and song syllables are shown in Figure 1. For one male the song repertoire analysis had to be performed across two consecutive recordings as neither of the recordings had the 25 song phrases necessary for a complete analysis.

The song analyses were done using Raven Pro 1.3 (Cornell Lab of Ornithology, http://www.birds.cornell.edu/raven/). Each recording was looked through and the locations of each song phrase in the recording were saved to a selection table plain-text file. The spectrograms of 25 consecutive song phrases, showing the frequency range from 0 up to 10500 Hz on the vertical axis and showing 2.5 seconds of recording time on the horizontal axis (Figure 1), were subsequently printed out on a black and white laser printer.
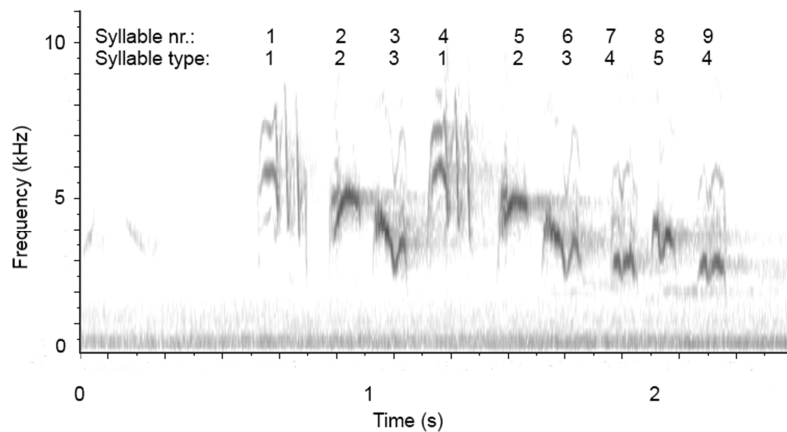

Figure 1 Spectrogram of a strophe from a recording of a pied flycatcher male. This strophe contained 9 syllables, and 5 syllable types.

Song syllables were identified by their visual appearance on the spectrogram. Additional identification was made through listening to the recording at both normal and 20% of normal speed to be able to recognize features of a song syllable that would be difficult to hear for a human at the normal speed, since a pied flycatcher female would likely be able to hear the difference at normal speed due to her perceptual sensitivity to the song of the males of her species (Knudsen and Gentner 2010).

To facilitate cataloguing, an alphanumeric numbering system was used where song syllables that were to some degree similar to each other were assigned the same number but a different letter, giving them a unique entry in the catalogue while enabling easier record-keeping and locating of song syllables during the song analyses. The repertoire comparisons treat each syllable catalogue entry as unique, disregarding any instances of syllables that are similar but not exactly the same, so that song syllable sharing is not overestimated. Some variation in the expression of song syllables was still allowed. Examples of syllable catalogue entries are shown in Figure 2. At the end of the cataloguing phase the catalogue held 584 entries, distributed across 393 unique song syllables.
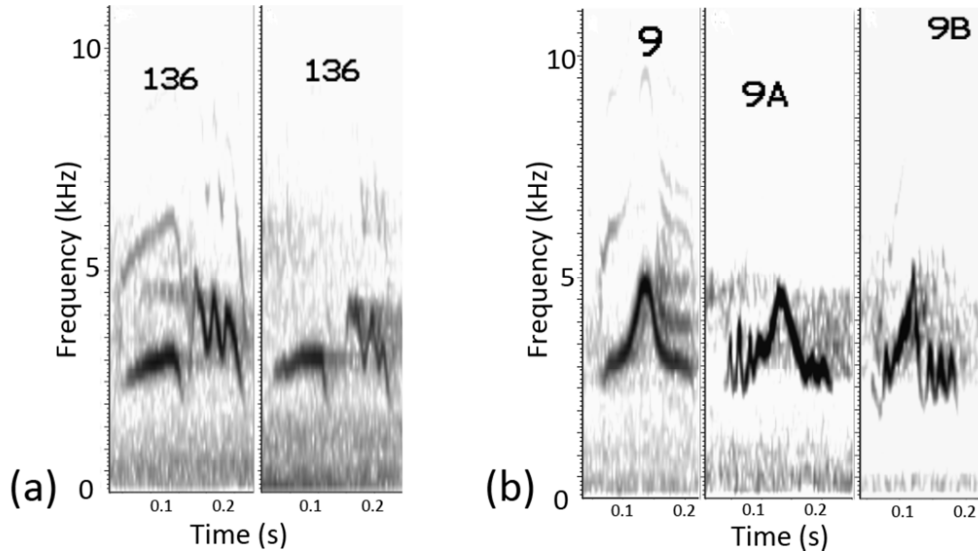
Figure 2 (a) shows the same unique song syllable catalogue entry, as sung by two different males. (b) shows unique catalog entries for three similar song syllables.

Repertoire comparisons

Each male's syllable repertoire was compared with every other male's syllable repertoire, to uncover any shared song syllables. A coefficient of repertoire similarity (RS) was calculated using the formula RS=Z/((X+Y)-Z) where Z is the number of shared song syllables between two males, X is the repertoire size of one male and Y is the repertoire size of the other male (Hultsch and Todt 1981). A RS value of 0 indicates no sharing while a value of 1 indicates sharing of all song syllables.

The proportion of song syllables a male shared with the population and with the group were calculated by dividing the number of song syllables he shared with the population by the total number of song syllables in the population, and by dividing the number of song syllables he shared with the group by the total number of song syllables found in the group.

To test for effects of recording date, the days from the first to the last recording were numbered sequentially, and for each pair of males the number of days between recording the first and recording the other (Nd) were calculated, using the following formula: $Nd = \sqrt{(RDx - RDy)^2}$ where RDx is the number value of the recording date for one male, and RDy is the number value for the recording date of the other, making Nd the number of days between recording one male and recording the other.

The song data was not normally distributed, so non-parametric methods were used for the analyses. Spearman's rank test was used to evaluate the significance of associations between two variables. The effect of one variable on two categories was Mann-Whitney U tested, while the effect of one variable on three or more categories was tested using a Kruskal-Wallis one-way analysis of variance (Holmes et al. 2011).

All statistical analyses were performed in PAST (Hammer et al. 2001).

Results

Repertoires and song syllable sharing

Of the 393 unique song syllables recorded, 77 were found in the repertoires of more than one male. A single song syllable was shared among 11 males, but most of the shared song syllables were only found in the repertoires of two or three males (Figure 3). 42.9% of the shared song syllables were shared by two males, and an additional 23.4% were shared by three males.
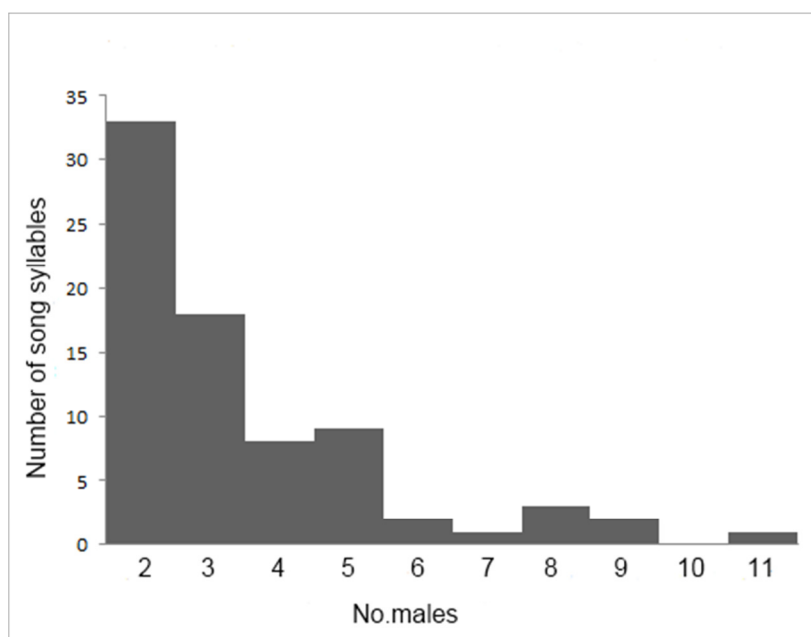

Figure 3 The number of song syllables shared by males (n=18).

Among the 18 recorded males, the repertoire size was 32.4±15.0 (mean ±SD, range 13-50) song syllables. The number of detected song syllables in a male's repertoire continued to increase throughout the 25 analyzed song strophes, suggesting that the catalogued repertoire did not contain all song syllables in the male's actual repertoire (Figure 4). The number of shared song syllables was 14.9±7.0 (mean±SD, range 7-27) and each male's repertoire featured 17.5±11.2 (mean±SD, range 3-40) unique song syllables that were not shared with any other male.

There was a highly significant correlation between the size of a male's repertoire and the number of song syllables he shared with other males in the population (Spearman's $r_s = 0.78$,

p < 0.001), and between the size of a male's repertoire and the number of unique song syllables in his repertoire ($r_s = 0.85$, p << 0.001). The number of song syllables a male shared with his group was strongly correlated with his repertoire size ($r_s = 0.69$, p = 0.001). There was no significant correlation between the number of shared song syllables and the number of unique song syllables ($r_s = 0.37$, p = 0.13).
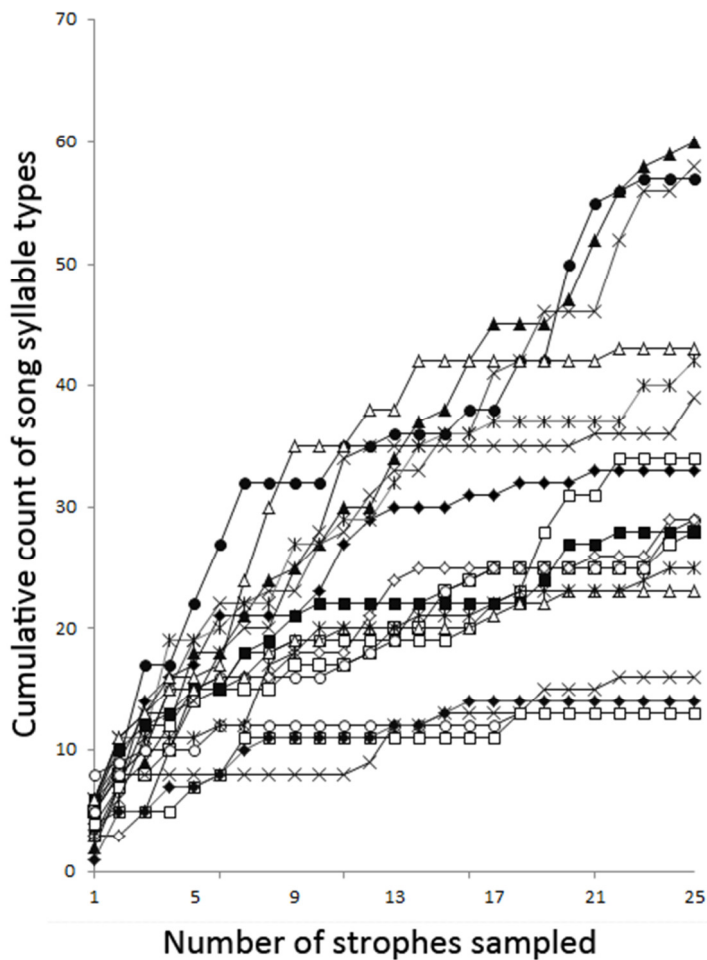
Figure 4 Repertoire curves for the recordings of the 18 flycatcher males in this study. Each curve represents one male, showing the increase in number of detected song syllables in the male's repertoire per strophe sampled.

Groups

Each of the four groups of males had 8.8±6.9 (mean±SD, range 3-18) song syllables which were unique to that group, not found in the repertoires of individuals in the other three groups. Each group shared 9.3±2.9 (mean±SD, range 7-37) song syllables with one or more of the other three groups. The members of each group shared 18±9.8 (mean±SD, range 10-31) song

syllables with each other, including those which were unique to the group and those the group shared with other groups. The recorded data is summarized in Table 1.

Table 1 Total song syllable pool, total shared song syllables and unique shared song syllables for each group, and number of song syllables the group shares with one or more groups.

	NG1	NG2	SG	IG
No. males	5	3	6	4
Total song syllable pool	227	111	178	68
Total song syllables shared within the group	31	10	20	11
Shared song syllables unique to the group	18	3	10	4
Song syllables shared with other groups	13	7	10	7

There was a significant difference in the coefficient of repertoire sharing (RS) within the groups (Kruskal-Wallis H = 8.808, p = 0.032): this was further examined using multiple comparisons (Holmes et al. 2011), see Table 2. A significant difference (Q = 2.624, 0.01 < p < 0.05) was found between the means of the ranks of RS of groups NG1 and SG. NG1 had a RS of 0.136±0.041 (mean±SD, range 0.020-0.136), SG had a RS of 0.031±0.026 (mean±SD, range 0-0.075). The low number of males in NG2 may explain the lack of significant difference. IG was also similar in RS to NG1, which was contrary to what was expected for the control group. Since the males of IG were not neighbors they were expected to have a significantly lower RS than the other groups, and this was not the case.

Table 2 Multiple comparisons examining the differences in RS in the four groups.

		NG1 $mean_{ranks}$=22.25	NG2 $mean_{ranks}$=19	SG $mean_{ranks}$=11.9	IG $mean_{ranks}$=22.83
NG1	Difference between means		3.25	10.35	0.58
	Q		0.511	**2.624**	0.117
NG2	Difference between means			7.1	3.83
	Q			1.621	0.561
SG	Difference between means				10.39
	Q				2.343
IG	Difference between means				
	Q				

Inexperienced males and experienced tutors

Repertoire size, number of shared song syllables and number of unique song syllables were tested with experience as a grouping variable. Experience was not a significant variable on the number of unique song syllables (Mann-Whitney $U = 29$, $p = 0.54$), near significant on repertoire size ($U = 15$, $p = 0.054$), but it was strongly significant on the number of shared syllables ($U = 5$, $p = 0.004$). The experienced males shared 21.8 ± 2.0 (mean $\pm$SD, range 13-27) song syllables with other males, while the inexperienced males only shared 11.5 ± 5.0 (mean $\pm$SD, range 7-21) song syllables. Checking for possible effects of repertoire size between inexperienced and experienced males, the percentage of a male's repertoire that he shared with others was also tested. Experience was not a significant variable on the percentage of shared song symbols ($U = 19.5$, $p = 0.13$).

The proportions of song syllables shared with the population and with the group were evaluated using experience as grouping valuable, the resulting U and p-values are shown in Table 3. Significant differences were found between experienced and inexperienced males in all comparisons except the one for proportion of song syllables shared with the group. Both experienced and inexperienced males had a higher proportion of song syllables shared with the group than with the population, and the experienced males had a higher proportion of song syllables shared with the population than the inexperienced males.

Table 3 Results of Mann-Whitney U tests on the proportion of shared song syllables with the population and with the group, using experience as grouping value.

Comparisons		Results	$n_1=$	$n_2=$
Population$_{Experienced}$	Population$_{Inexperienced}$	$U = 5$, $p = 0.004$	6	12
Population$_{Experienced}$	Group$_{Experienced}$	$U = 5$, $p = 0.045$	6	6
Population$_{Inexperienced}$	Group$_{Inexperienced}$	$U = 29$, $p = 0.014$	12	12
Group$_{Experienced}$	Group$_{Inexperienced}$	$U = 22$, $p = 0.205$	6	12

Proportion of shared song syllables

To test the first prediction of the hypothesis that the inexperienced males learned from experienced tutors within their own group, the proportions of song syllables shared with the population and with the group were evaluated using the assigned groups as grouping variable. There was a significant difference found in group NG1 ($U = 2$, $p = 0.036$), but not in SG ($U =$

12, p = 0.38), NG2 (U = 2, p = 0.38) or IG (U = 1, p = 0.059). NG1 had a higher proportion of song syllables shared with the group (0.082±0.023, mean±SD, range 0.049-0.104) than with the population (0.050±0.017, mean±SD, range 0.030-0.069). IG, which was expected to have a higher proportion of song syllables shared with the population than the group due to the lack of an experienced tutor and geographical closeness to the other group members, had a higher proportion of song syllables shared with the group (0.109±0.057, mean±SD, range 0.036-0.164) than with the population (0.028±0.017, mean±SD, range 0.018-0.053), though the difference was not significant. Only the NG1 result supported the hypothesis, the rest being contrary to the first prediction that the proportion of shared song syllables with the group should be higher than the proportion shared with the population. The overall conclusion must be that the hypothesis was not supported by these results.

Coefficient of repertoire sharing – groups

To test the second prediction the RS of each group were compared to the RS of the whole population. No significant difference was found for IG (U = 300.5, p = 0.15), SG (U = 847, p = 0.09) nor NG2 (U = 186.5, p = 0.58) and only a near significant difference for NG1 (U = 487, p = 0.055). The second prediction was not met, as none of the groups had a RS distribution significantly different from the population, and the hypothesis was not supported by these results.

Coefficient of repertoire sharing – inexperienced and experienced neighbors

The third prediction was tested comparing RS between inexperienced and experienced neighbors and non-neighbors. No significant difference was found when comparing the RS between inexperienced neighbors and RS between inexperienced and experienced neighbors (U = 85.5, p = 0.64). The RS between experienced neighbors was not significantly different from the RS between inexperienced and experienced neighbors (U = 11, p = 0.16), and only near significantly different from the RS between inexperienced neighbors (U = 4, p = 0.051). RS between inexperienced males and experienced neighbors and RS between inexperienced males and experienced non-neighbors was not significant (U = 206, p = 0.81). The means, standard deviations and min/max values for the RS distributions are given in Table 4. The inexperienced males did not have a significantly different RS with the experienced males of

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their group than with any of the other males, so the third prediction was not met and the hypothesis was not supported.

Table 4 A summary of the descriptive statistics for the coefficient of sharing, RS, between males of the listed experience types.

	Mean	SD	Min	Max	n=
Experienced+Experienced neighbors	0.091	0.016	0.074	0.106	3
Inexperienced+Inexperienced neighbors	0.044	0.034	0	0.125	12
Experienced+Inexperienced neighbors	0.053	0.043	0	0.136	16
Inexperienced+Experienced non-neighbors	0.048	0.038	0	0.189	27

Differences in learning between inexperienced adults and juveniles

Repertoire size, number of shared song syllables and number of unique song syllables were tested with age as a grouping variable. Age was not a significant variable on repertoire size (U = 24.5, p = 0.17), though it was significant on the number of shared syllables (U = 15, p = 0.026), but not significant at all on the number of unique song syllables (U = 40, p = 1).

Adult males shared 18.9±2 (mean±SD, range 7-27) song syllables with other males while juveniles shared 11±1.7 (mean±SD, range 7-21) song syllables with other males. There was no significant difference in the percentage of song syllables adults or juveniles shared with other males (U = 19.5, p = 0.07).

Coefficient of repertoire sharing – inexperienced adults and juveniles

In order to test the hypothesis that there is a difference in song learning between inexperienced adults and juveniles, RS was compared between adult and juvenile neighbors. Comparing RS between adult neighbors and RS between juvenile neighbors showed no significant difference (U = 10, p = 0.073). The RS between juvenile neighbors was not significantly different from the RS between juvenile and adult neighbors (U = 61, p = 0.64), but the RS between adult neighbors was highly significantly different from the RS between juvenile and adult neighbors (U = 19.5, p = 0.006). Inexperienced adults differed significantly from juveniles in their RS with experienced neighbors (U = 5, p = 0.025) (Figure 5). The

means, standard deviations and min/max values for the RS distributions are given in Table 5. Contrary to the prediction that juveniles should have higher RS with experienced tutors than inexperienced adults, the inexperienced adults were the ones with the higher RS with experienced tutors. The prediction isn't met, but the general hypothesis that there is a difference in song learning between inexperienced adults and juveniles is supported.
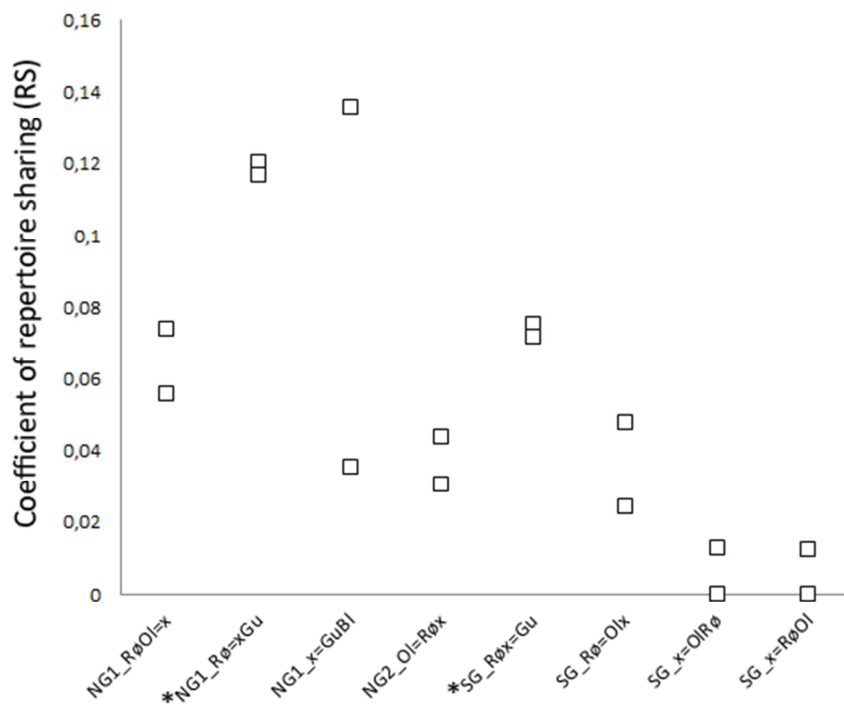
Figure 5 The inexperienced males of the three neighbor groups, showing each male's RS with the two experienced males in his group. * indicates inexperienced adults.

Table 5 A summary of the descriptive statistics for the coefficient of sharing, RS, for the five comparisons between juveniles and adults.

	Mean	SD	Min	Max	n=
Adult+Adult neighbors	0.094	0.021	0.071	0.120	7
Juvenile+Juvenile neighbors	0.048	0.062	0	0.171	7
Adult+Juvenile neighbors	0.046	0.037	0	0.136	20
Inexperienced Adults+Experienced neighbors	0.096	0.026	0.071	0.120	4
Juveniles+Experienced neighbors	0.039	0.038	0	0.136	12

Time between recordings

The average time which passed between recordings of two males was 11.6±8.4 (mean±SD, range 0-31) days. Differences in the number of days between the recordings of pairs of males (Nd) across groups were not significant (H = 3.405, p = 0.333).

A significant correlation between Nd and the coefficient of repertoire sharing (RS) was found in SG (r_s = -0.52, p = 0.049), which was the group with the lowest average Nd (6.53±4.207, mean±SD, range 1-15), but no such correlation was found in the other three groups. There was no correlation between Nd and RS between neighbors (r_s = 0.007, p = 0.970) or across the whole population (r_s = -0.031, p = 0.707), so the hypothesis that there would be an effect of time between recordings of different males on the observed song syllable sharing was not supported by these findings.

Discussion

Sharing of song syllables between inexperienced and experienced neighbors

Males were assigned to one of four groups based on geographical location and access to experienced neighbors that might function as tutors. There was a significant difference in coefficient of repertoire sharing (RS) between the males of two of the three neighbor groups, and each group including the control had several shared song syllables which were not found within the rest of the population. The control group had a similar amount of unique shared song syllables as the smallest group of neighbors. This may be because while the control group males were not neighbors within 100m of each other, two of the males were recorded at nest boxes in a fairly open area where song may travel further, and may have heard each other's song. Sounds become more difficult to hear the further away the listener is from the source and birdsong is no exception. Dense forests or other complex environments may cause distortion in the sound, while open landscapes would be more conducive to transmitting the song across longer distances before they eventually degrade (Catchpole and Slater 2008). Another possible reason for the similar amount of unique shared song syllables between the control group and the smallest group of neighbors is that the unique song syllables had been learned independently in the each of the control group males, though this seems much less likely than two of those males being close enough to hear each other sing. The possibility that the control group males were close enough to each other to hear and learn song syllables was not considered in the analyses.

When looking at the whole population, both experienced and inexperienced males had a higher proportion of song syllables shared with the group than with the population, and the experienced males had a higher proportion of song syllables shared with the population than the inexperienced males. This finding was not reflected in the analysis of the proportion of song syllables shared with the group or population by neighbor group, with one exception. This may be due to the larger syllable repertoire of experienced males, which may overlap with other males of the study area, representing song syllable learning of previous years.

Field studies have many challenges, particularly the difficulty of establishing experimental controls when one cannot control all the variables (Rivera-Gutierrez et al. 2011). The males examined in this study were not confined to a single location and could have overheard males other than their neighbors before their song was recorded. And since they were only recorded once, it's difficult to say anything about who learned from whom.

Repertoire sharing among neighbors is found in several species. The song sparrow *Melospiza melodia* male uses repertoire sharing to selectively match the repertoire of his neighbor when replying to the neighbor's song (Beecher et al. 1996). The chowchilla *Orthonyx spaldingii* showed high levels of song syllable sharing between neighboring groups, and a sharp drop in sharing past a 1km boundary. Neighbor groups were used in that study because individuals of the same group sang identical song, so it was impossible to identify them any closer from song alone. (Koetz et al. 2007). Great tits *Parus major* were found to add songs to their repertoire learned from newly arrived neighbors as adults (McGregor and Krebs 1989). Male indigo buntings *Passerina cyanea* in adjacent territories share some or even all song syllables with their neighbors, forming song neighborhoods in which males used the same or similar song syllables (Beckett and Ritchison 2010).

Sharing with direct neighbors can be beneficial or detrimental. In species with male-male song interaction sharing of song syllables may signal aggression or function as a threat, or lack of sharing can be used to identify a stranger entering the area (Beecher and Brenowitz 2005).

Differences in learning between adults and juveniles

A significant difference in learning between inexperienced adults and juveniles was found in this study. Inexperienced adults had a higher RS with experienced males than the juveniles did, which was contrary to what was expected. The sensitive phase for learning in most songbirds is when they're young, with sensitivity declining as the bird approaches adult song (Catchpole and Slater 2008). In this study the inexperienced adults were shown to share a significant amount of song syllables with the experienced tutors, and unlike the juveniles the two inexperienced adults with access to experienced tutors had almost equal RS with both tutors in their neighbor group.

While the pied flycatchers have been found to incorporate new song syllables into their song during the same season that they learned them (Eriksen et al. 2011), this is not the case in all birds. In the common nightingale *Luscinia megarhyncos* song types which are learned after the juvenile males reach full song, so-called crystallization of the repertoire, are not used until the next season, and the males keep song types that are sung by more birds in the population, eliminating uncommon songs (Todt and Geberzahn 2003; Kiefer et al. 2010) It is possible the juveniles learned more song syllables from the tutors than they sang, or that they did not sing all of the song syllables they had learned at the time they were recorded.

The effect of time between recordings

There was no significant correlation found between the coefficient of repertoire sharing (RS) and the number of days between recording one male and recording another (Nd), except for within the group of males which had the lowest values of both. While this group was not significantly different from the others in Nd, it had a significantly different RS. The correlation between low Nd and low RS suggests that there may be a minimum amount of time required to learn song syllables from a neighbor. This would be consistent with the findings of Eriksen et al. (2011), where the males who learned from the playback stimulus had only learned one syllable type each over the span of one week.

Two of the three males in the smallest neighbor group were recorded on the same day, and if there is a minimum amount of time necessary to learn song syllables as suggested by the comparison of RS and Nd, this may have caused a lack of observed song syllable sharing. In fact the inexperienced male of this group, who was one of the two males recorded on the same day, had the lowest amount of group-shared song syllables of the males found in the population except for one of the control group males. It is possible the male had learned more song syllables and was not using them at the time of recording.

Each male was only recorded once, and it is possible that recording the males a second time might have uncovered more details about their song syllable repertoires, and thus given a better overview of the song syllable sharing in the population. Pied flycatcher males reduce their singing activity dramatically once mated (Lundberg and Alatalo 1992). The number of song syllables is reduced and the song is composed of a different set of song syllables than it

was before mating (Espmark and Lampe 1993). Accounting for arrival date and mating date of the males might have explained some of the findings, since a male wouldn't learn song syllables from the repertoires of males whose song he was never exposed to.

Social interaction is important in the song learning process for several songbirds, and direct social contact with a partner was a major element in song development for European starling *Sturnus vulgaris* nestlings, where the song of individuals who had been raised in isolation was incomplete, with elements missing or produced differently from normal (Poirier et al. 2004). Male song sparrows *Melospiza melodia* were able to learn from multiple tutors in a lab experiment simulating field conditions, and they preferentially learned song types which were shared between the tutors, though whether that was due to increased exposure to the same song type or due to the fact that the song type was shared by several tutors and may serve some crucial function was not uncovered (Nordby et al. 2000). A later study on the same species did not support the hypothesis that birds are more likely to hear songs they hear more (Nulty et al. 2010).

Male mountain white-crowned sparrows *Zonotrichia leucophrys oriantha* are born with a genetic predisposition toward the song of their own subspecies, processing it differently than other song they overhear, which helps them distinguish between potential tutors to choose one of their own subspecies to learn from (Nelson 2000).

Song syllable cataloguing may have been either too restrictive, thus underestimating the number of shared syllables, or too non-restrictive, leading to the overestimation of the same. Only 25 consecutive song strophes were analyzed and the results suggest the recorded repertoire was only a subset of the total repertoire of the males. While this may be a good amount of song strophes to analyze other song variables, it may not be sufficient for an accurate comparison of shared song syllables in the pied flycatcher.

A longitudinal study of song learning among pied flycatchers might shed more light on the question of who learns from whom, though as their song syllable repertoires can change from one year to the next (Espmark and Lampe 1993) this may be difficult to assess. In the study of vocal plasticity and open-ended learning in pied flycatchers by Eriksen et al. (2011) none of the males who had learned a song syllable in 2007 included it in their repertoires the following year. Interestingly though, the two syllables males did learn in that study resembled song syllables which were catalogued in this study, from recordings made three years later.

This suggests a study conducted over several years may give some insight into sharing of song syllables that a short-term study will not.

Conclusion

The neighbor group analyses on inexperienced males and experienced tutors consistently identified NG1 as significantly or near significantly different from the others. This group had the largest song syllable pool, and the largest amount of group-shared and group-unique song syllables. The relationships between the groups were largely not significant and must be due to some variable that was not evaluated in this study. Large repertoire size may explain the findings for NG1, but explanations for the lack of significance in neighbor analyses in general have to be found elsewhere. Perhaps in the arrival date and length of exposure to tutor song, or in analysis of a larger number of consecutive song phrases. The apparent significance between low number of days between recording, which could possibly be inferred as a lack of exposure if they are correlated with the days of arrival, and low correlation of repertoire sharing in SG suggests the existence of a minimum of exposure time required for song learning to occur.

Evidence of song learning using experienced males as tutors was only found in inexperienced adults. The two inexperienced adults with access to experienced tutors had a higher coefficient of sharing with both experienced tutors in their neighbor group, something which was not found among any of the juveniles. The results of this study suggest inexperienced adults may be adjusting their repertoires to resemble that of their experienced neighbors, either by learning new song syllables or using song syllables they already know which are found among the experienced neighbors.

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