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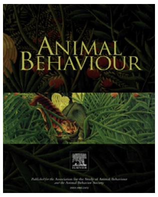

Song sparrows do not learn more songs from aggressive tutors

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Birdsong has long been a prominent model system for studying learning of vocal signals. However, despite widespread acknowledgment of the importance of social factors in shaping birdsong learning, few studies have attempted to parse out and analyse specific social variables in a naturalistic context. Here we report a field study of song learning in song sparrows, *Melospiza melodia*, which tests the role of a specific social factor, the aggressiveness of potential song tutors. The hypothesis that young birds may learn more from more aggressive tutors was proposed over three decades ago, but has only been tested in laboratory studies, and with mixed results. We assayed aggression and signalling of potential tutors through repeated playback experiments in the field during the song-learning period of a cohort of young sparrows. We also recorded these young birds and traced their repertoires back to potential tutors. We asked whether consistent individual differences in aggressive and signalling behaviours of tutors would predict the degree to which their songs were learned by young birds in the cohort of the year. We sampled more than half of the adult male (potential tutor) population and almost all of the young males (tutees), and replicated the results of a previous study on this same population concerning which songs were learned from which tutors. However, we found no effect of the aggressiveness of potential tutors, their levels of their aggressive signalling or their level of normal singing on their tutoring success. In short, young song sparrows do not learn more from aggressive tutors. We argue for further research on other social factors under natural conditions.

Although vocal communication is widespread in animals, learning of vocal signals is comparatively rare. To date, only a few taxa have been shown to learn their vocalizations, including some bats (Boughman, 1998), cetaceans (Janik & Slater, 1997; Reiss & McCowan, 1993), humans (but no other primates), and at least three orders of birds: parrots (Pepperberg, 1994), hummingbirds (Baptista & Schuchmann, 1990; Gaunt, Baptista, Sanchez, & Hernandez, 1994), and most prominently, songbirds (Beecher & Brenowitz, 2005; Brenowitz & Beecher, 2005; Catchpole & Slater, 2008). Vocal learning has been most intensively studied in humans and songbirds.

The many parallels between language learning and song learning were first noted by Marler (1970). These include the presence of an early sensitive period, a predisposition to learn species-specific vocalizations, an early subsong or babbling stage, and the necessity of auditory feedback for development but not maintenance of vocalizations in adults, to name a few. Still another parallel discovered more recently is the importance of social factors in vocal learning.

The role of social factors in song learning was first noted in the classic ‘live tutor experiments’ by Baptista and Petrinovich (1984, 1986) that used live birds as opposed to pre-recorded songs played back from a speaker as learning models. A general finding in these and subsequent live-tutor experiments was that live tutors are much more effective than tape tutors, presumably due to the social context that live tutors provide and that tape-tutors cannot (see reviews in: Beecher & Burt, 2004; Nelson, 1997). Very few studies, however, have attempted to analyse exactly which social factors are important in promoting song learning.

It seems likely that social factors play a crucial role in determining how a young bird selects the songs that he will incorporate into his repertoire. Even laboratory studies with live tutors present only a few tutors at most to the young tutees, and even then only in a very artificial situation. The context for song learning in the wild of course will be very different. Consider song learning by a young song sparrow, *Melospiza melodia*, male living in a resident population, like our study population in Washington state. During his first year of his life, when he learns and finalizes his song repertoire (Nordby, Campbell, & Beecher, 2002), he hears hundreds of unique songs from 30 to 40 males, but ends up retaining only about eight to

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nine or so of these (Beecher, Campbell, & Stoddard, 1994; Nordby, Campbell, & Beecher, 1999; Templeton, Reed, Campbell, & Beecher, 2012). Furthermore, often a tutee learns most of his songs from a single ('primary' tutor) male; on average, the primary tutor accounts for about half of a tutee's repertoire (Nordby et al., 1999). How then does the young sparrow choose the birds from which he will learn his songs and the particular songs of these birds that he will retain in his final repertoire?

Aggressiveness of Tutors as a Potential Social Factor

A key fact about song learning is that the period of song learning in many species is correlated with the period of territory establishment by a young male (Beecher et al., 1994; DeWolfe, Baptista, & Petrinovich, 1989; Kroodsma, 1974; Liu & Kroodsma, 2006; Payne, 1981). During this period, the tutees engage in aggressive interactions with potential tutors (Arcese, 1989; Nice, 1943; Payne, 1981). Therefore, it is plausible that aggressive interactions with older neighbours during territory establishment would play a role in shaping the final repertoire of a young bird.

Although a newcomer has to engage multiple opponents over the course of establishing a territory and negotiating boundaries, some of these opponents are more likely to be aggressive than others. It is a now well established that individuals show consistent differences in aggressiveness, which is generally part of the behavioural syndrome, or personality of animals (Bell, Hankison, & Laslowski, 2009; Sih, Bell, & Johnson, 2004). These individual differences in aggression are likely to be important in determining the nature and intensity of interactions of territory owners with newcomers. Specifically, a territory holder with an aggressive personality would be expected to engage in higher-intensity interactions with a newcomer than would another territory holder with a less aggressive personality. These differing intensities of interaction then could be reflected in the song-learning preferences, either positive or negative, of the tutee.

Aggressiveness of tutors may affect song learning at both proximate and ultimate levels. At the ultimate (functional) level, it may be advantageous to learn songs primarily from the more aggressive tutors because during and after territory establishment the young bird would be expected to have more frequent and intense interactions with these neighbours. Shared songs would be expected to be more effective in mediating these interactions (and perhaps these songs would be more effective with other neighbours as well). There is strong evidence that aggressiveness is an individually consistent personality trait in song sparrows (Akçay, Campbell, & Beecher, 2014; Hyman, Hughes, Searcy, & Nowicki, 2004; Nowicki, Searcy, Krueger, & Hughes, 2002). Furthermore, neighbouring birds have been shown to be sensitive to each other's aggressiveness in this species, responding more aggressively to their aggressive neighbours (Akçay, Wood, Searcy, Templeton, Campbell, & Beecher, 2009; Hyman et al., 2004).

There is also extensive evidence in western song sparrows that songs shared with neighbours are used preferentially to mediate aggressive interactions (Akçay, Tom, Campbell, & Beecher, 2013; Beecher, Stoddard, Campbell, & Horning, 1996; Burt, Campbell, & Beecher, 2001). Given these lines of evidence, it is likely that the ability to mediate potentially costly interactions with an aggressive neighbour via shared songs would be beneficial for a bird, and thus, a strategy that maximizes sharing with more aggressive tutors might be adaptive.

At the proximate level, a tutee may learn more songs from aggressive tutors simply because the tutee may interact with aggressive tutors at a higher rate and/or may hear aggressive tutors interact with other males more frequently through eavesdropping (Beecher, Burt, O'Loghlen, Templeton, & Campbell, 2007; Templeton, Akçay, Campbell, & Beecher, 2010). Such a 'dosage effect' would tilt repertoires of young tutees towards more aggressive males. Note that it is also possible in principle that tutees may avoid aggressive tutors, although a tutee cannot go on avoiding every aggressive individual indefinitely if he is to get a territory. To the contrary, successful territorial challengers (which are the ones who go on to crystallize their repertoire and sing) start challenging territorial owners as early as August of their hatch year and in many cases are at least as aggressive in simulated intrusions as older birds (Akçay, Campbell, & Beecher, n.d.).

Although Payne's (1981) studies with indigo buntings, *Passerina cyanea*, first highlighted the potential influence of tutor aggressiveness on song learning, no field study to date has tested the relationship between aggression and song learning. Indeed, the only studies explicitly relating aggression to song learning have been laboratory studies. In the first study testing the relationship between aggression and song learning, Payne (1981) found that captive indigo buntings preferentially learned their songs from tutors with whom they could interact socially (as opposed to only hearing). These interactions often involved aggression (chasing and supplanting each other), although the design of the experiments did not allow for distinguishing the effect of aggression from the potential effects of other types of social interactions. In another study, Clayton (1987) found that zebra finches, *Taeniopygia guttata*, learned preferentially from tutors that were more aggressive to them. Importantly, in this experiment it was not the overall level tutor aggression (i.e. irrespective of the tutee), but the rate of aggressive interactions specifically between a particular tutor and a particular tutee that predicted song learning. Another study by Jones and Slater (1996) found that zebra finches tended to learn more from aggressive tutors, although the investigators could not tease apart the effect of the overall level of tutor aggression from the effect of the specific aggressive interactions between the tutor and tutee. Although the laboratory studies reviewed above showed some support for the aggression hypothesis, a study by Williams (1990) failed to find an effect of aggression on the number of syllables copied from the tutor, again in zebra finches. Finally, Casey and Baker (1993) reported that young white-crowned sparrows, *Zonotrichia leucophrys*, failed to develop normal song when the only tutor that was available to them was an aggressive male, suggesting that aggression may have an inhibitory effect on song learning. However, tutee and tutor were housed together, so the tutee could not escape from the tutor and was subjected to rather severe aggression.

In summary, the laboratory studies that specifically tested the relationship between tutor aggression and song learning have given inconsistent results, which is perhaps not surprising given the restrictive social environment and the differences in housing conditions between the studies. Furthermore, the laboratory setting is different in many regards from the natural setting, including the fact that the young birds in a laboratory setting do not have the option of ending an aggressive interaction, making extrapolation to song learning in the wild a difficult proposition. It is for this reason that we decided to test the aggression hypothesis in the wild.

An important point to take away from the previous research is that there are two rather different versions of the aggression hypothesis. The first version, which we test here, focuses on aggressiveness as an individually consistent trait (as it is found to be in many species; Bell et al., 2009): according to this version, which we term the general aggression hypothesis, tutors that are generally more aggressive will be more effective (or more preferred) tutors. According to the second, nonmutually exclusive, version of the aggressiveness hypothesis, it is the specific level of aggression between a particular tutee and a particular tutor that will determine the effectiveness of a tutor (as found in Clayton's study of zebra finches). We term this the specific aggression hypothesis.

Here we report the first study to examine the relationship between aggression and song learning in a wild population of songbirds. We focus on consistent individual differences in the aggressive and signalling behaviours of song sparrows. We quantified these behaviours in a sample of potential song tutors (adult male territory holders) via repeated tests through autumn 2009 and winter/spring 2010. We then correlated the tutors' aggression levels and aggressive signalling behaviours with the song learning of a cohort of tutees that hatched in spring 2009 and held territories in spring 2010. Based on the aggression hypothesis, we predicted that tutees would learn more songs from more aggressive tutors than they would from less aggressive tutors.

METHODS

Study Site and Subjects

We studied song sparrows breeding in Discovery Park, Seattle, WA, U.S.A. as part of a long-term study that has been ongoing since 1986 (Beecher, 2008; Beecher et al., 1994; Nordby et al., 1999). We captured song sparrows with mist nets either passively or using playback and banded them with U.S. Fish and Wildlife Service metal bands and a unique combination of three coloured leg bands that allowed visual identification of individuals later.

Males hold territories year-round in this population and hatch-year males begin defending territories sometime between August of their hatch year and the following spring (Nordby et al., 1999). This period coincides with the song-learning period, which starts early in the first summer and lasts at least into autumn and potentially into the next spring (Nordby, Campbell, & Beecher, 2001; Nulty et al., 2010).

The cohort of first-year males consisted of 43 birds that hatched in 2009 and held territories in the study area in spring 2010. We identified these males as ‘second-year’ (SY) based on their banding history (i.e. banded as juveniles, identified by their plumage, or at their nest before September 2009, $N = 21$), or by their subsong or plastic song after September 2009 ($N = 22$); adult males do not sing subsong or plastic song. A further 10 SY males were observed to be holding territories briefly in spring, but they disappeared (probably predated) before they could be recorded. Finally, three more SY males were recorded but their songs apparently originated from outside the study area as they could not be traced back to any tutors in the population (all three of these SY males were at the very edge of the study area). The song sparrows in our population crystallize their repertoire and sing fully formed adult songs by March or April (Beecher et al., 1994), such that SY males that establish their first territories and older males that move into the study area from the edges to replace depredated males cannot be distinguished by song after this point. Predation in early spring is common (Akçay et al., 2012). Therefore, any unbanded bird first seen in the study area on or after 1 March was excluded from the analysis; we excluded eight such males.

We considered all adult males present in June 2009 (the hatch year of our subjects) as potential tutors. Out of 123 males that held territories in June 2009, we were able to record 119; the remaining four disappeared before they could be recorded. Territories of tutors and tutees were surveyed at least once every 2 weeks throughout September and October 2009 and January to April of 2010 to check for survival of territory owners, shifting of territories and appearance of new birds. We considered a territory owner to have disappeared if he was not observed in his territory or in any of the nearby territories and his entire territory was being actively defended by other birds.

Recording and Song Analysis

Male song sparrows sing eight to nine song types, on average (range 6–13), and deliver these songs in bouts, singing one song type several times before switching to another song type (‘eventual variety’). We recorded the full repertoire of all the tutees and potential tutors using Marantz PMD 660 digital recorders and Sennheiser ME66/K6 shotgun microphones. Repertoires were considered to be fully recorded when we recorded at least 16 consecutive song switches from each male. In our population, the average number of switches required to record the entire repertoire is 10.9, with a median value of 11 and a range of 6–16 (Beecher, Wilkinson, Campbell, & Nordby, n.d.). Several of the tutees were recorded in February, before their repertoire fully crystallized, but because birds at this stage already sing readily identifiable song types we included them in the comparisons. The main change between February repertoire and fully crystallized repertoire is that the young birds sometimes drop a song type in a process of selective attrition (Nordby, Campbell, & Beecher, 2007).

Song analyses were carried out as described in detail by Nordby et al. (1999). Briefly, for each male we printed out spectrograms of several variations of each song type, including major variants (Syrinx, John Burt, www.syrinxpc.com). Each tutee song was compared visually with all of the potential tutors' songs by three or four judges (Fig. 1). To do this, we laid out the repertoire of the tutee on a large table, and each judge went through the tutor repertoires and laid out matching songs next to the tutee songs on the table. Subsequently, each judge independently went through these to identify the best matches to the tutee songs. After this scoring stage, the judges discussed their best match judgments and arrived at a consensus score sheet where all judges agreed upon all the tutor matches (before this step, judges agreed on 75.2% of best matches).

If a single male was identified as having the best match to the tutee song, he was given a ‘tutor score’ of 1 (i.e. full credit) for that song on the grounds of parsimony. In many cases, the song type was shared among several tutors, as song sharing is common in this population (Hill, Campbell, Nordby, Burt, & Beecher, 1999), and in some cases, two or more potential tutors had equally good matches. This occurred when (1) the tutors' songs were virtually identical, or (2) one tutor matched one variation better, while the other tutor matched another variation better, or (3) one tutor's song was a better match in one respect (say the introductory notes) and the other tutor's song was a better match in another respect (say a terminal trill). In these cases, credit was split among the tutors (0.5 each if there were two tutors, 0.33 each of there were three, etc.; see Results for percentages of songs where credit was split in this way). The bottom two rows of Fig. 1 show one such split-credit case: here each variation of the same tutee song type matched a different tutor better, and so each tutor got 0.5 credit for that song. Figure 2 shows two examples where a matching song did not merit credit for tutorship. Our method corresponds to the ‘inclusive’ analysis reported by Nordby et al. (1999). Note that the two methods used by Nordby et al. led to identical conclusions in all respects except for the number of tutors.

For each tutor male we calculated his total ‘tutor score’ as the sum of all the tutor credit he got across all the tutees. For instance, if a tutor got credit for tutoring five songs for one tutee, two songs for another, and 0.5 songs each for two more, his total tutor score would be 8. This measure gives us an overall metric of how effective a tutor a male was or of tutees' ‘preference’ for that tutor.

Playback Experiments

We carried out repeated playbacks to assay aggression and aggressive signalling in the territories of potential tutor males

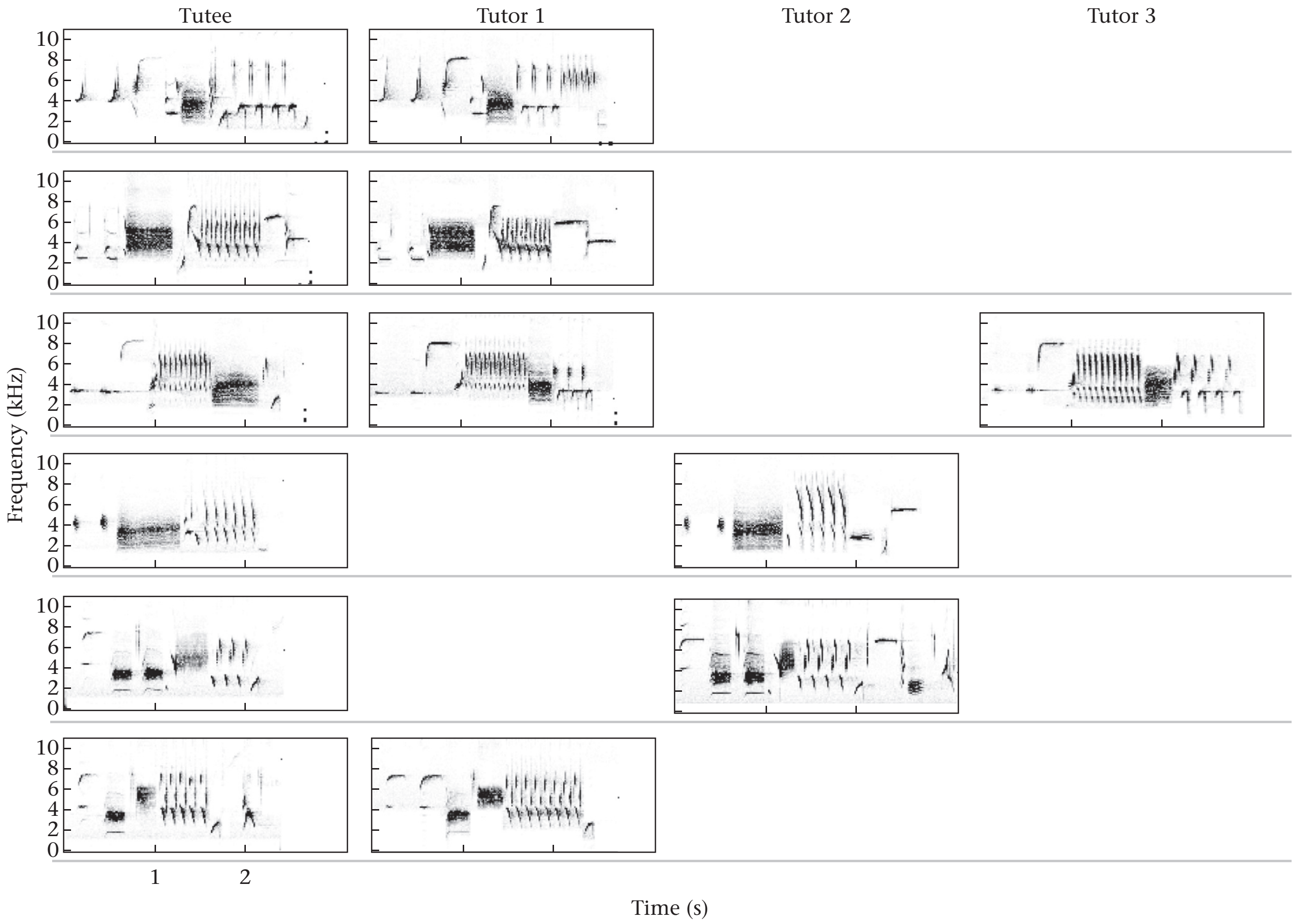

Figure 1. A partial repertoire of a tutee (five out of nine songs), with three out of five matching tutors. The bottom two rows show two major variations of the same song type that the tutee had in his repertoire. For this variation, tutor 1 and tutor 2 each shared 0.5 credit, as one of the major variations matched tutor 1, whereas the other matched tutor 2.

between September 2009 and May 2010. Given that at the time of the playbacks we did not know the tutor scores of any of the tutors, we sought to sample as many potential tutors as possible. A detailed analysis of these playback assays is reported in Akçay, Campbell, et al. (2014). Briefly, we carried out these tests in five separate time periods (September 2009, October 2009, January 2010, February 2010 and May 2010) and tested a total of 69 males (out of 123, 56% of all potential tutors) at least once (11 subjects tested once, 13 subjects tested twice, 12 subjects tested three times, 19 subjects tested four times and 14 subjects tested five times).

The playbacks were carried out from the territory centre using a Pignose speaker connected to an iPod via a 20 m cable. Each

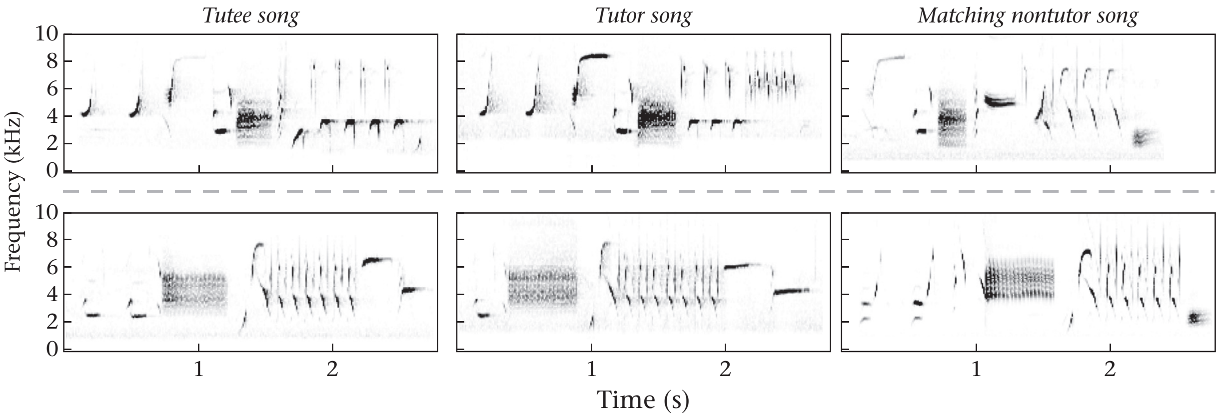

Figure 2. Two typical examples illustrating cases where a matching song did not get tutor credit. The left column shows two tutee songs, the middle column shows tutor songs that provided the best match to the two tutee songs (i.e. matched all elements in the tutee songs), and the right column shows matching songs that did not merit tutor credit according to our analysis (i.e. mismatched one or more elements in the tutee songs).

playback lasted 10 min, during which two song types from the subject's own repertoire (self song) were broadcast for 5 min each, at a rate of four songs/min. Two observers standing 20 m from the speaker noted the following behaviours: flights, distance of the bird from the speaker at each flight, soft songs, wing waves and loud songs. One of the observers recorded the trial (the vocal behaviour of subject and the trial narration, including the behaviours listed above) using the same recording equipment as above.

Response Measures for Aggression Assays

Using Syrinx, we extracted the following measures of aggressive response from the trial recordings: rate of flights, closest approach to the speaker during the playback and time spent within 5 m of the speaker. These three measures were highly correlated with each other; we therefore entered them into a principal component analysis (PCA) and took the first component (aggressive behaviour, PCA1) as the aggressive behaviour score (see Table 1 for the coefficients).

We also extracted the following signalling behaviours: rate of loud (normal) songs, rate of soft songs and rate of wing waves. Soft songs and wing waves are aggressive signals that reliably predict attack on a taxidermic mount (Akçay et al., 2013; Akçay, Tom, Holmes, Campbell, & Beecher, 2011; Searcy, Anderson, & Nowicki, 2006), and were highly correlated with each other; they are often given in a single ‘puff-sing-wave’ display (Nice, 1943). We therefore entered these two into a PCA and took the first component (aggressive signalling, PCA1) as the aggressive signalling score. Loud song rates do not reliably predict attack in this species (Searcy et al., 2006; Searcy & Beecher, 2009), but loud song is important in broadcasting territory ownership and indicating territory borders. Given that juveniles likely eavesdrop on broadcast singing (Templeton et al., 2010; Templeton et al., 2012), loud song rates of males might also be expected to predict tutoring success.

All of the response measures were highly repeatable (repeatabilities are given in Table 2; see also Akçay, Campbell, et al., 2014). We therefore took the average scores for each male to arrive at a single score for each of the response variables. We should note that the individual differences were stable beyond the period of the playback assays considered here. In Akçay, Campbell, et al. (2014), we report that the average aggressive behaviour and aggressive signalling scores in 2009–2010 (the same ones reported here) predicted whether subjects would attack a taxidermic mount in spring 2011 (more aggressive males were more likely to attack the mount).

Data Analyses

The primary purpose of this study was to determine whether there is a relationship between general aggressiveness of a tutor and the degree to which young birds copy his songs. To answer this question we carried out two parallel analyses. In the first, for all adult males for whom we had aggressive response, signalling response and overall tutor scores, we correlated each of the response scores (aggressive behaviour scores, aggressive signalling scores and loud song rates) with the tutor scores. In these analyses, we excluded adult males that did not survive to 1 January 2010 ($N = 7$), because in our previous studies (Nordby et al., 1999) we found that tutor males that did not survive past 1 January had much lower tutor scores than those that did survive beyond this date (see also Results). This left a sample size of 62 tutor males (50.4% of 123 tutors in the population).

Our second analysis derives from the fact that young birds frequently learn the majority of their songs from one tutor (Nordby et al., 1999). We designated the ‘primary tutor’ as the adult male from whom the tutee learned the most; on average, that tutor accounted for approximately half of the tutee's songs (see Results). This primary tutor is almost always a neighbour or a bird that the tutee has replaced (Nordby et al., 1999). In our second analysis, we therefore compared the aggressive and signalling behaviours of the primary tutor for each tutee with those of another bird in that neighbourhood chosen at random that did not tutor more than a single song of the tutee in question (for simplicity, we call the latter ‘nontutor’ in this comparison, although he may have tutored one song for that tutee, and he may have tutored other birds). For the purposes of this analysis, we considered only primary tutors that tutored at least four of the tutee's songs; 25 out of 43 tutees had a primary tutor so defined. In cases where two tutees had the same primary tutor (there were four such cases), we included the primary tutor only once, bringing the final sample size for the pairwise comparisons between primary tutors and nontutors to 21 pairs. Of these 21 pairs, we had data on aggressive and signalling behaviours of 16 pairs. We compared the aggressive and signalling behaviours of primary tutors and nontutors via paired t tests.

In addition to the above analyses we sought to replicate the major findings on the pattern of song learning reported in Nordby et al. (1999) for the 1992 cohort of tutees. To this end, we compared the tutees in 1992 (Nordby et al., 1999) and 2009 (present study) cohorts with respect to (1) their repertoire sizes, (2) the number of tutors each tutee had and (3) the proportion of the repertoire learned from the primary tutor, using unpaired t tests. We also asked whether two main findings of Nordby et al. would hold for the 2009 cohort: (1) whether tutors that survived past 1 January of the second year of the tutees tutored more songs than nonsurvivors and (2) whether the influence of the primary tutor was affected by the proximity of his territory to his tutee's. For the first question, we compared the tutor scores of males that survived past 1 January 2010 with those that did not with an unpaired t test. For the second question we compared primary tutors that were neighbours (sharing a boundary or having only one intervening territory or an open area between their territories, $N = 32$) with non-neighbours (at least two intervening territories between primary tutor and tutee, $N = 9$). Two of the primary tutors did not survive into 2010;

Table 1
Loading coefficients for the principal component analyses (PCA)

Variable	Coefficients	
	Aggressive behaviour PCA	Aggressive signalling PCA
Rate of flights	0.81	
Time spent within 5 m	0.87	
Closest approach	−0.79	
Rate of soft songs		0.83
Rate of wing waves		0.83

The first component of PCA on aggressive behaviours (the top three variables) explained 67.9% of variance and was taken as the aggressive behaviour score. The first component of PCA on aggressive signalling behaviours (the bottom two variables) explained 68.3% of variance and was taken as the aggressive signalling score. $N = 219$ trials, $N = 69$.

Table 2
Repeatabilities, significance and 95% confidence intervals for tutor aggressive behaviour scores, aggressive signalling scores and loud song rates (from Akçay, Campbell, et al., 2014)

Variable	Repeatability	*P*	95% CI
Aggressive behaviour score	0.48	<0.0001	0.35, 0.62
Aggressive signalling score	0.57	<0.0001	0.45, 0.70
Loud song rate	0.37	<0.001	0.23, 0.51

Repeatabilities were calculated using R package ‘rpt’ by Nagakawa and Schielzeth (2010).

in both cases the tutee acquired at least part of the tutor's territory; these two cases were excluded from this analysis.

All analyses were carried out either in Excel or R (R Development Core Team, 2012). In addition to the statistical tests, we also report the effect sizes and 95% confidence intervals (CI) associated with the comparisons.

RESULTS

We attempted to trace 390 songs from 43 tutees (average repertoire size = 9.07) and were able to trace all but 24 (6.2%) of the songs to a tutor in the population. For 193 songs (53.5% of 366 songs that were traced), tutorship was assigned to a single tutor, for 127 songs (34.7%), tutorship was split between two tutors, and for 43 songs (11.7%), tutorship was split between three or more tutors. Overall, the song learning of tutees in the 2009 cohort closely followed the pattern reported for the 1992 cohort in Nordby et al. (1999; see Table 3 for comparisons of the cohorts). Out of 119 potential tutors that were recorded, 88 (73.9%) had nonzero tutor scores, meaning they were implicated in at least one song. Similar to the 1992 cohort, the tutees in the 2009 cohort, on average, learned 4.56 songs (50.3% of the average repertoire size) from their primary tutors, although individual tutees differed greatly in how many songs they learned from their primary tutors (range 1–11 songs). The only major difference between the two cohorts of tutees was the average repertoire size, which was about one song larger for the 2009 cohort than for the 1992 cohort (Table 3). This difference is probably partly due to the fact that that we included some birds recorded only in early spring before they had dropped one or two songs to arrive at their final repertoire (Nordby et al., 2007). These birds had disappeared by late spring. Note, however, that the observed repertoire size was within the range reported for our population (lower range: 8.1 songs, Nordby et al., 1999; upper range: 9.2 songs, Beecher, Campbell, Burt, Hill, & Nordby, 2000).

As in the earlier study, we found that potential tutor males that survived past 1 January 2010 (the second calendar year of the tutees) tutored more songs, on average, than the males that did not survive (mean ± SD tutor score: survivors: 3.51 ± 4.13, $N = 93$; nonsurvivors: 1.52 ± 2.82, $N = 26$ males; $t_{117} = 2.78$, $P = 0.006$).

Finally, as Nordby et al. (1999) found for the 1992 cohort, tutees learned more from their primary tutor when they were direct neighbours with this tutor (average ± SD proportion of the repertoire learned from the primary tutor: 0.54 ± 0.19, $N = 32$) than when they were not neighbours (0.30 ± 0.13, $N = 9$) ($t_{39} = 3.55$, $P = 0.001$).

Overall Tutor Scores, Aggression and Signalling

There were no significant correlations between the tutor scores of the 62 tutors and either their aggressive behaviour scores (Pearson correlation: $r_{60} = -0.06$, $P = 0.62$; 95% CI: −0.32, 0.19; Fig. 3a), their aggressive signalling scores ($r_{60} = 0.06$, $P = 0.64$, $N = 62$; 95% CI: −0.19, 0.32; Fig. 3b) or their loud song rates ($r_{60} = 0.02$, $P = 0.85$, $N = 62$; 95% CI: −0.23, 0.27; Fig. 3c).

Table 3
Comparison of song learning data from 1992 cohort (Nordby et al., 1999, their inclusive analysis, reported in their Table 1) and 2009 cohort (this study)

Variability	1992 cohort	2009 cohort	t_{80}	P
Number of potential tutors	122	123		
Number tutors identified	87	88		
Number of tutees	39	43		
Tutee repertoire size	8.12 (1.32)	9.07 (1.42)	**3.09**	**0.003**
Number of tutors per tutee	5.47 (2.00)	4.82 (2.14)	1.40	0.16
Number of songs learned from primary tutor	4.01 (1.81)	4.56 (2.15)	1.23	0.22

Means (±SD) are given for the bottom three rows for both cohorts, and the cohorts are compared with unpaired *t* test. Values in bold denote a significant difference between cohorts.

Primary Tutors versus Nontutors

Primary tutors and nontutors did not differ in terms of their aggressive behaviour scores ($t_{15} = 0.59$, $P = 0.56$, Cohen's $d = 0.19$, 95% CI: −0.44, 0.82; Fig. 4a), their aggressive signalling scores ($t_{15} = 1.16$, $P = 0.26$, $d = 0.43$, 95% CI: −0.34, 1.18; Fig. 4b), or their loud song rates ($t_{15} = 0.35$, $P = 0.73$, $d = 0.14$, 95% CI: −0.63, 0.90; Fig. 4c).

DISCUSSION

In this study, we tested the hypothesis that aggressiveness and aggressive signalling behaviours of a tutor are important determinants of which songs young birds will learn from which older birds. We found that although males showed highly consistent individual differences in aggressive and signalling behaviours, none of these differences predicted either their overall tutoring success or whether they became a primary tutor to a tutee. This null finding is particularly strong as we sampled aggressive and signalling behaviours of more than half of the potential tutors, and we were able to trace almost all of the songs of the tutee cohort to their tutors. Furthermore, the pattern of song learning very closely replicates our previous findings for this population (Nordby et al., 1999).

These results thus do not support the hypothesis that more aggressive birds will be more effective song tutors (or that young birds will preferentially learn from more aggressive tutors) for song sparrows in our population. Note that the reverse was not true: tutees also did not prefer nonaggressive tutors. Given that this is only the first study to explicitly test any version of the aggression hypothesis for song learning in the field, further research certainly is warranted before one can claim that aggressiveness (at least as construed as an individually consistent trait) of a tutor is not an important social factor in song learning in general. There is certainly a need for more research on social factors in the field to test the aggression hypothesis (or any other hypotheses concerning social factors in song learning).

New Hypotheses on the Role of Social Interaction in Tutor Choice

Although we have ruled out consistent individual differences in tutor aggressiveness as a critical factor in determining which songs of which tutors a young bird learns, our field studies do reveal a pattern of song learning that is far from random. In both the 1992 cohort reported in Nordby et al. (1999) and the 2009 cohort reported here, song learning followed the same pattern: birds tended to learn from several tutors but tended to skew their repertoire towards one particular tutor (the primary tutor), which, on average, accounted for about half of the songs in the tutee's repertoire. The tutees of both 1992 and 2009 cohorts also learned more from primary tutors that were neighbours. The primary tutors were generally different for different tutees. In the current data set, out of 25 cases where there was a strong primary tutor (i.e. who accounted for four or more songs in the tutee's repertoire), only four tutors were primary tutors for more than one tutee. Looking at all 43 tutees, only seven of the primary tutors were shared between any tutees (and no tutor was a primary tutor for more than two tutees).

This pattern of tutor choice may be partly explained by the fact that tutees tend to learn from males that are their neighbours. Nevertheless, even taking proximity into account, tutor choice

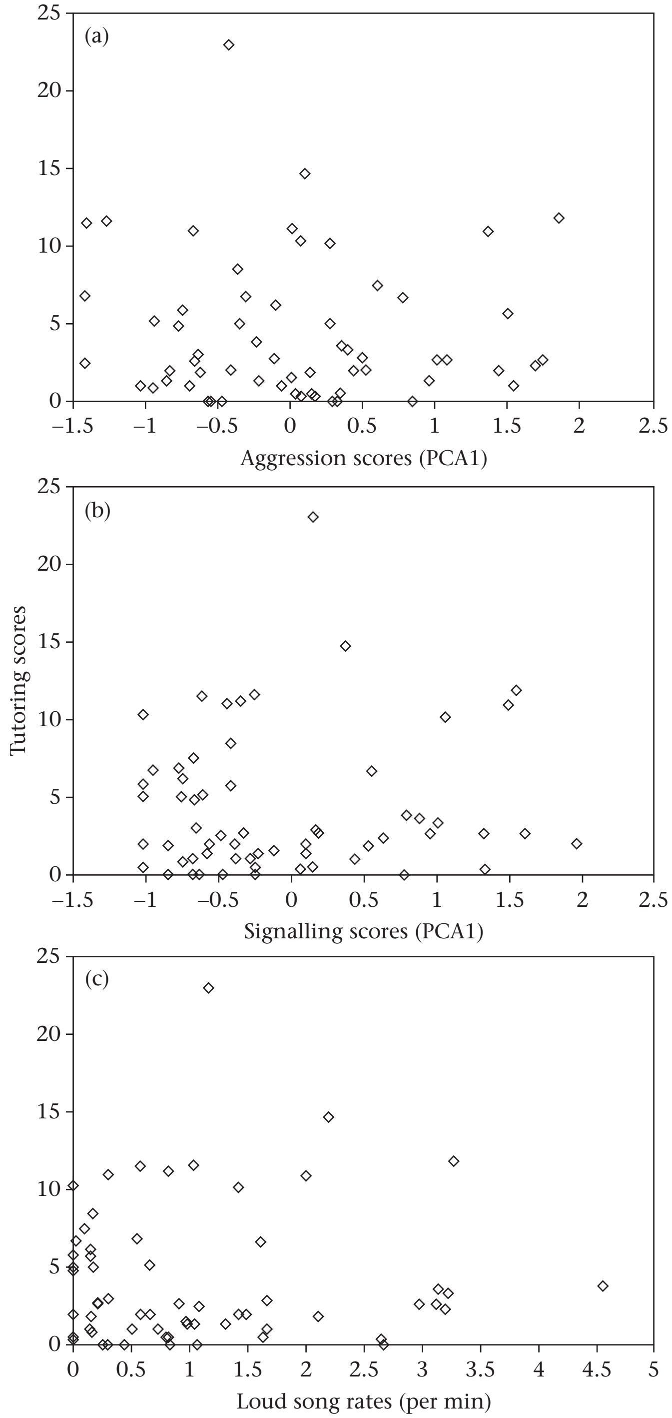

Figure 3. Scatterplots showing the associations (or lack thereof) of tutoring scores and (a) aggressive behaviour scores, (b) aggressive signalling scores and (c) loud song rates.

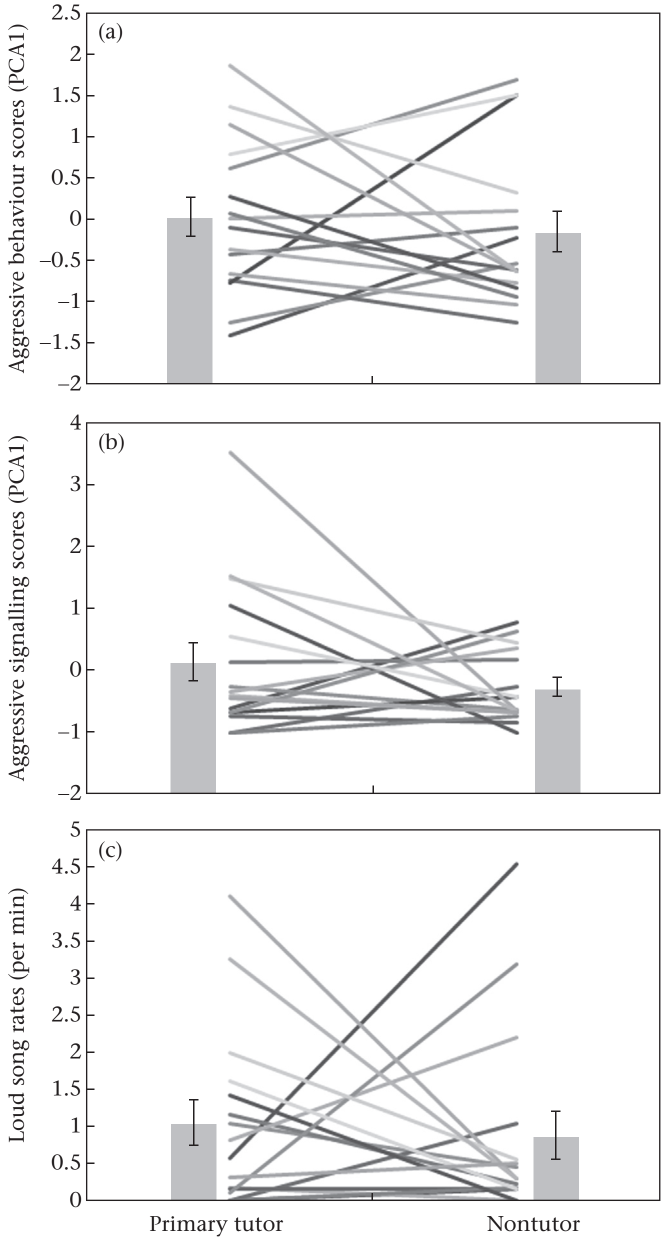

Figure 4. Paired comparisons between primary tutors and nontutors of 16 tutees in (a) aggressive behaviour scores, (b) aggressive signalling scores and (c) loud song rates. Bars show means ± SE; lines show single pairs of primary tutors and nontutors.

seems to be active given the disproportionate influence of the primary tutor, who after all is just one of several neighbours to each tutee (the median number of immediate neighbours of birds in our population is 4, range 3–6). Moreover, two tutees that settled near one another often picked a different older neighbour as their primary tutor. This suggests that whatever drives tutor choice, it is likely to be dependent on the nature of interactions between the tutee and tutors. As reviewed in the Introduction, one possibility is that it is not the consistent individual differences in overall aggression that matters in song learning, but rather the specific level of aggressive interactions between particular tutors and particular tutees (i.e. a tutor might be aggressive towards one tutee, but not towards another, and we did not attempt to take such measurements in this study). Specific aggressiveness of a tutor towards a specific tutee is more easily measured in the laboratory than in the field, and indeed, Clayton (1987) found it to be a better predictor of song learning in zebra finches than was the general (nonspecific) aggressiveness of the tutor. Related to this hypothesis, we have previously shown that although song sparrows show consistent individual differences in overall aggressiveness, they also adjust their aggression levels as appropriate to specific neighbours, by increasing their aggressiveness following simulated intrusions of a 'bad' neighbour onto their territory, or onto the territory of another neighbour (Akçay, Reed, Campbell, Templeton, & Beecher, 2010; Akçay et al., 2009). Thus, despite evidence for consistent individual differences in aggressiveness among these birds, aggression is still a plastic trait and it is perfectly plausible that a tutor might be more aggressive towards one tutee than towards another. According to this second version of the aggression hypothesis, then, tutees would learn more from tutors that are specifically more aggressive to them. Testing this hypothesis in the field will require detailed behavioural data to separate out general aggressiveness from specific aggressiveness directed at particular tutees.

Another hypothesis on the role of social interactions in tutor choice is what we call the 'dear tutor hypothesis'. According to this hypothesis, primary tutor choice depends critically on a dear enemy relationship, on mutual tolerance between the tutee and tutor. The dear enemy effect is common in many territorial systems (Temeles, 1994) and its nature varies, ranging from simply reduced aggression towards established neighbours compared to strangers (Stoddard, 1996) to active cooperative territory defence (Detto, Jennions, & Backwell, 2010; Elfström, 1997). Song sparrows in our population show the dear enemy effect (Stoddard, Beecher, Horning, & Campbell, 1991). There is also evidence in another western population of song sparrows that territory owners are less aggressive towards neighbours with whom they share more songs (Wilson & Vehrencamp, 2001). This finding suggests that if a primary tutor and a tutee show high levels of sharing, they may display reduced aggression towards each other as well. Finally, in our population, song sharing in the first year of territory tenure predicts how long a territory owner will be able to hold his territory (Beecher, Campbell, & Nordby, 2000), although it is not clear how much of the effect can be directly attributed to sharing between tutees and their tutors.

All the evidence reviewed in the previous paragraph points to a possible role of song learning in building a mutually beneficial relationship between a newly establishing young bird and an already established older male. Under the dear tutor hypothesis, then, tutees learn from tutors with whom they have established a cooperative dear enemy relationship. The idea that vocal learning reflects cooperative or affiliative relationships is not novel: many cooperatively breeding and group-living species show vocal sharing within cooperative groups (e.g. Akçay, Hambury, Arnold, Nevins, & Dickinson, 2014; Berg, Delgado, Cortopassi, Beissinger, & Bradbury, 2012; Greig, Taft, & Pruett-Jones, 2012; Keen, Meliza, & Rubenstein, 2013; Price, 1998). The dear tutor hypothesis is an extension of this idea to unrelated pairs of tutor–tutees that breed independently.

Testing both of these hypotheses requires detailed information on tutor–tutee interactions in the wild. Recent advances in tracking technology, such as interaction tags that can log encounters between two individuals (e.g. the Encounternet system developed by John Burt for this very purpose; Mennill et al., 2012; Rutz et al., 2012), would allow for detailed mapping of the frequency of interactions between potential tutors and tutees. Furthermore, with the advent of affordable and logistically feasible acoustic recording arrays (Blumstein et al., 2011), acoustic interactions between tutors and tutees can be mapped in more detail. However, given that interactions between tutors and tutees can be aggressive or nonaggressive, the critical test for the hypotheses listed above will still have to rely on detailed observational studies and playback experiments that aim to measure tutee aggressiveness towards particular tutors and vice versa. We have started doing these experiments in our Seattle population.

In summary we argue that further work on social factors in song learning requires more detailed studies on social interactions between tutors and tutees during the period of song learning and territory establishment. Although field studies do not afford the experimental control inherent in laboratory studies, we think that most of the hypotheses on social factors in song learning are most realistically tested in the field.

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References

Akçay, Ç., Campbell, S.E., & Beecher, M.D. (n.d.). Territory defense by juvenile song sparrows. Unpublished raw data.

Akçay, Ç., Campbell, S. E., & Beecher, M. D. (2014). Individual differences affect honest signalling in a songbird. *Proceedings of the Royal Society B: Biological Sciences, 281*, 20132496.

Akçay, Ç., Hambury, K. L., Arnold, J. A., Nevins, A. M., & Dickinson, J. L. (2014). Song sharing with neighbours and relatives in a cooperatively breeding songbird. *Animal Behaviour, 92*, 55–62.

Akçay, Ç., Reed, V. A., Campbell, S. E., Templeton, C. N., & Beecher, M. D. (2010). Indirect reciprocity: song sparrows distrust aggressive neighbours based on eavesdropping. *Animal Behaviour, 80*, 1041–1047.

Akçay, Ç., Searcy, W. A., Campbell, S. E., Reed, V. A., Templeton, C. N., Hardwick, K. M., et al. (2012). Who initiates extra-pair mating in song sparrows? *Behavioral Ecology, 23*, 44–50.

Akçay, Ç., Tom, M. E., Campbell, S. E., & Beecher, M. D. (2013). Song type matching is an honest early threat signal in a hierarchical animal communication system. *Proceedings of the Royal Society B: Biological Sciences, 280*, 20122517.

Akçay, Ç., Tom, M. E., Holmes, D., Campbell, S. E., & Beecher, M. D. (2011). Sing softly and carry a big stick: signals of aggressive intent in song sparrows. *Animal Behaviour, 82*, 377–382.

Akçay, Ç., Wood, W. E., Searcy, W. A., Templeton, C. N., Campbell, S. E., & Beecher, M. D. (2009). Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals. *Animal Behaviour, 78*, 97–102.

Arcese, P. (1989). Territory acquisition and loss in male song sparrows. *Animal Behaviour, 37*, 45–55.

Baptista, L. F., & Petrinovich, L. (1984). Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. *Animal Behaviour, 32*, 172–181.

Baptista, L. F., & Petrinovich, L. (1986). Song development in the white-crowned sparrow: social factors and sex differences. *Animal Behaviour, 34*, 1359–1371.

Baptista, L. F., & Schuchmann, K. L. (1990). Song learning in the Anna hummingbird (*Calypte anna*). *Ethology, 84*, 15–26.

Beecher, M. D. (2008). Function and mechanisms of song learning in song sparrows. *Advances in the Study of Behavior, 38*, 167–225.

Beecher, M. D., & Brenowitz, E. A. (2005). Functional aspects of song learning in birds. *Trends in Ecology & Evolution, 20*, 143–149.

Beecher, M. D., & Burt, J. M. (2004). The role of social interaction in bird song learning. *Current Directions in Psychological Science, 13*, 224–228.

Beecher, M. D., Burt, J. M., O'Loghlen, A. L., Templeton, C. N., & Campbell, S. E. (2007). Bird song learning in an eavesdropping context. *Animal Behaviour, 73*, 929–935.

Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E., & Nordby, J. C. (2000). Song type matching between neighbouring song sparrows. *Animal Behaviour, 59*, 21–27.

Beecher, M. D., Campbell, S. E., & Nordby, J. C. (2000). Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal Behaviour, 59*, 29–37.

Beecher, M. D., Campbell, S. E., & Stoddard, P. K. (1994). Correlation of song learning and territory establishment strategies in the song sparrow. *Proceedings of National Academy of Sciences of the United States of America, 91*, 1450–1454.

Beecher, M. D., Stoddard, P. K., Campbell, S. E., & Horning, C. L. (1996). Repertoire matching between neighbouring song sparrows. *Animal Behaviour, 51*, 917–923.

Beecher, M.D., Wilkinson, G.S., Campbell, S.E., & Nordby, J.C. (n.d.). Song type switching and matching during free singing in song sparrows. Unpublished raw data.

Bell, A., Hankison, S. J., & Laslowski, K. L. (2009). The repeatability of behavior: a meta-analysis. *Animal Behaviour, 77*, 771–783.

Berg, K. S., Delgado, S., Cortopassi, K. A., Beissinger, S. R., & Bradbury, J. W. (2012). Vertical transmission of learned signatures in a wild parrot. *Proceedings of the Royal Society B: Biological Sciences, 279*, 585–591.

Blumstein, D. T., Mennill, D. J., Clemins, P., Girod, L., Yao, K., Patricelli, G., et al. (2011). Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. *Journal of Applied Ecology, 48*, 758–767.

Boughman, J. W. (1998). Vocal learning by greater spear–nosed bats. *Proceedings of the Royal Society B: Biological Sciences, 265*, 227–233.

Brenowitz, E. A., & Beecher, M. D. (2005). Song learning in birds: diversity and plasticity, opportunities and challenges. *Trends in Neurosciences, 28*, 127–132.

Burt, J. M., Campbell, S. E., & Beecher, M. D. (2001). Song type matching as threat: a test using interactive playback. *Animal Behaviour, 62*, 1163–1170.

Casey, R. M., & Baker, M. C. (1993). Aggression and song development in white-crowned sparrows. *Condor, 95*, 723–728.

Catchpole, C. K., & Slater, P. J. B. (2008). *Bird song: Biological themes and variations*. Cambridge, U.K.: Cambridge University Press.

Clayton, N. S. (1987). Song tutor choice in zebra finches. *Animal Behaviour, 35*, 714–721.

Detto, T., Jennions, M. D., & Backwell, P. R. Y. (2010). When and why do territorial coalitions occur? Experimental evidence from a fiddler crab. *American Naturalist, 175*, E119–E125.

DeWolfe, B. B., Baptista, L. F., & Petrinovich, L. (1989). Song development and territory establishment in Nuttall's white-crowned sparrows. *Condor, 91*, 397–406.

Elfström, S. T. (1997). Fighting behaviour and strategy of rock pipit, *Anthus petrosus*, neighbours: cooperative defence. *Animal Behaviour, 54*, 535–542.

Gaunt, S. L. L., Baptista, L. F., Sanchez, J. E., & Hernandez, D. (1994). Song learning as evidenced from song sharing in two hummingbird species (*Colibri coruscans* and *C. thalassinus*). *Auk, 111*, 87–103.

Greig, E. I., Taft, B. N., & Pruett-Jones, S. (2012). Sons learn songs from their social fathers in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences, 279*, 3154–3160.

Hill, C. E., Campbell, S. E., Nordby, J. C., Burt, J. M., & Beecher, M. D. (1999). Song sharing in two populations of song sparrows (*Melospiza melodia*). *Behavioral Ecology and Sociobiology, 46*, 341–349.

Hyman, J., Hughes, M., Searcy, W. A., & Nowicki, S. (2004). Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure and neighbor aggressiveness. *Behaviour, 141*, 15–27.

Janik, V. M., & Slater, P. J. B. (1997). Vocal learning in mammals. *Advances in the Study of Behavior, 26*, 59–99.

Jones, A. E., & Slater, P. J. B. (1996). The role of aggression in song tutor choice in the zebra finch: cause or effect? *Behaviour, 133*, 103–115.

Keen, S. C., Meliza, C. D., & Rubenstein, D. R. (2013). Flight calls signal group and individual identity but not kinship in a cooperatively breeding bird. *Behavioral Ecology, 24*, 1279–1285.

Kroodsma, D. E. (1974). Song learning, dialects, and dispersal in the Bewick's wren. *Zeitschrift für Tierpsychologie, 35*, 352–380.

Liu, W.-C., & Kroodsma, D. E. (2006). Song learning by chipping sparrows: when, where, and from whom? *Condor, 108*, 509–517.

Marler, P. (1970). Birdsong and speech development: could there be parallels? *American Scientist, 58*, 669–673.

Mennill, D. J., Doucet, S. M., Ward, K. A. A., Maynard, D. F., Otis, B., & Burt, J. M. (2012). A novel digital telemetry system for tracking wild animals: a field test for studying mate choice in a lekking tropical bird. *Methods in Ecology and Evolution, 3*, 663–672.

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews, 85*, 935–956.

Nelson, D. A. (1997). Social interaction and sensitive phases for song learning: a critical review. In C. T. Snowdon, & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 7–22). Cambridge, U.K.: Cambridge University Press.

Nice, M. M. (1943). Studies in the life history of the song sparrow II. The behavior of the song sparrow and other passerines. *Transactions of the Linnean Society of New York, 6*, 1–328.

Nordby, J. C., Campbell, S. E., & Beecher, M. D. (1999). Ecological correlates of song learning in song sparrows. *Behavioral Ecology, 10*, 287–297.

Nordby, J. C., Campbell, S. E., & Beecher, M. D. (2001). Late song learning in song sparrows. *Animal Behaviour, 61*, 835–846.

Nordby, J. C., Campbell, S. E., & Beecher, M. D. (2002). Adult song sparrows do not alter their song repertoires. *Ethology, 108*, 39–50.

Nordby, J. C., Campbell, S. E., & Beecher, M. D. (2007). Selective attrition and individual song repertoire development in song sparrows. *Animal Behaviour, 74*, 1413–1418.

Nowicki, S., Searcy, W. A., Krueger, T., & Hughes, M. (2002). Individual variation in response to simulated territorial challenge among territory-holding song sparrows. *Journal of Avian Biology, 33*, 253–259.

Nulty, B., Burt, J. M., Akçay, Ç., Templeton, C. N., Campbell, S. E., & Beecher, M. D. (2010). Song learning in song sparrows: relative importance of autumn vs. spring tutoring. *Ethology, 116*, 653–661.

Payne, R. B. (1981). Song learning and social interaction in indigo buntings. *Animal Behaviour, 29*, 688–697.

Pepperberg, I. M. (1994). Vocal learning in grey parrots (*Psittacus erithacus*): effects of social interaction, reference, and context. *Auk, 111*, 300–313.

Price, J. J. (1998). Family- and sex-specific vocal traditions in a cooperatively breeding songbird. *Proceedings of the Royal Society B: Biological Sciences, 265*, 497–502.

R Development Core Team. (2012). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reiss, D., & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. *Journal of Comparative Psychology, 107*, 301–312.

Rutz, C., Burns, Z. T., James, R., Ismar, S. M., Burt, J., Otis, B., et al. (2012). Automated mapping of social networks in wild birds. *Current Biology, 22*, R669–R671.

Searcy, W. A., Anderson, R. C., & Nowicki, S. (2006). Bird song as a signal of aggressive intent. *Behavioral Ecology and Sociobiology, 60*, 234–241.

Searcy, W. A., & Beecher, M. D. (2009). Song as an aggressive signal in songbirds. *Animal Behaviour, 78*, 1281–1292.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution, 19*, 372–378.

Stoddard, P. K. (1996). Vocal recognition of neighbors by territorial passerines. In D. E. Kroodsma, & D. E. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 356–374). Ithaca, NY: Cornell University Press.

Stoddard, P. K., Beecher, M. D., Horning, C. L., & Campbell, S. E. (1991). Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. *Behavioral Ecology and Sociobiology, 29*, 211–215.

Temeles, E. (1994). The role of neighbours in territorial systems: when are they 'dear enemies'? *Animal Behaviour, 47*, 339–350.

Templeton, C. N., Akçay, Ç., Campbell, S. E., & Beecher, M. D. (2010). Juvenile sparrows preferentially eavesdrop on adult song interactions. *Proceedings of the Royal Society B: Biological Sciences, 277*, 447–453.

Templeton, C. N., Reed, V. A., Campbell, S. E., & Beecher, M. D. (2012). Spatial movements and social networks in juvenile male song sparrows. *Behavioral Ecology, 23*, 141–152.

Williams, H. (1990). Models for song learning in the zebra finch: fathers or others? *Animal Behaviour, 39*, 745–757.

Wilson, P. L., & Vehrencamp, S. L. (2001). A test of the deceptive mimicry hypothesis in song-sharing song sparrows. *Animal Behaviour, 62*, 1197–1205.