



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.

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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, & Petrino, 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'Loughlen, 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 of 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

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