Animal Behaviour 129 (2017) 223–228

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Good tutors are not dear enemies in song sparrows

Çağlar Akçay [a, *], S. Elizabeth Campbell [b], Michael D. Beecher [b, c]

[a] Department of Biological Sciences, Virginia Tech, Blacksburg, VA, U.S.A.
[b] Department of Psychology, University of Washington, Seattle, WA, U.S.A.
[c] Department of Biology, University of Washington, Seattle, WA, U.S.A.

ARTICLE INFO

Article history:
Received 28 February 2017
Initial acceptance 27 March 2017
Final acceptance 1 May 2017

MS. number: A17-00198R

Keywords:
aggression
communication
cooperation
social learning
song learning

Birdsong is the most widely studied example of vocal learning outside human language and shares important parallels with it, including the importance of social factors during development. Our understanding of how social factors affect song learning, however, remains surprisingly incomplete. Here we examine the possible role of aggressive interactions in determining song 'tutor' choice in song sparrows, *Melospiza melodia*, a songbird in which individuals display song learning strategies ranging from learning primarily from one tutor, to learning a few songs each from a number of tutors. We test two hypotheses: the competition hypothesis suggests that young birds learn more from tutors with whom they compete especially intensely and predicts that tutees will respond with high aggression to tutor songs. In contrast, the cooperation hypothesis suggests that song learning reflects a cooperative relationship between the tutor and the tutee and predicts that tutees will respond with low aggression to tutor songs. In a playback experiment we found that birds responded more aggressively to songs of their tutors than they did to songs of strangers and that the strength of aggressive response correlated positively with how much they had learned from that tutor. These results provide the first field evidence for the hypothesis that young males preferentially learn their songs from adult males with whom they compete most intensely during the song-learning phase, and perhaps afterwards.

Although vocal communication is ubiquitous in the animal kingdom, social learning of vocal signals is limited to a few taxa, including humans (but not other primates), cetaceans, bats, elephants and three orders of birds (Baptista & Schuchmann, 1990; Boughman, 1998; Marler & Tamura, 1964; Pepperberg, 1994; Reiss & McCowan, 1993). Of these, song in songbirds is the best studied system next to human language (Beecher & Brenowitz, 2005; Catchpole & Slater, 2008).

Early studies showed striking parallels between the development of vocal signals in humans and songbirds including an early sensitive period, a predisposition to learn conspecific vocalizations, a babbling (or subsong) stage, and the necessity of auditory feedback for normal development (Marler, 1970). Another parallel is the social nature of vocal development. Although the social aspect of vocal development is obvious for humans, the potent role of social interactions in song learning was not fully appreciated until laboratory studies used live birds as song 'tutors' rather than recorded song as had been conventional (Baptista & Petrinovich, 1984, 1986). Although it is now widely accepted that song learning is a social process in which young birds (tutees) hear and engage in interactions with adults (tutors), there is a dearth of studies attempting to identify the critical social factors (Beecher, 2008).

Despite the many striking parallels between human and songbird vocal learning, the key social factors in vocal learning may be quite different for the two taxa. In particular, whereas the tutor–tutee (teacher–student) relationship in humans is clearly a cooperative one, with both parties typically related, the common case in songbirds is that tutor and tutee are unrelated competitors. This is because most songbirds commence song learning only after they disperse from their natal area, and thus their song tutors are their future territorial competitors rather than their parents, usually fathers (here and throughout the rest of paper we focus on male song and use the male pronoun, but note that female singing is common in other species, particularly in the tropics; Riebel, Hall, & Langmore, 2005). Species where fathers act as song tutors for their sons are rare (Grant & Grant, 1996; Greig, Taft, & Pruett-Jones, 2012; Immelmann, 1969). Instead, in most songbirds, song tutors are unrelated adults, some of whom will be their territorial competitors during the next breeding season (Beecher & Brenowitz, 2005; Brenowitz & Beecher, 2005). This point can be illustrated

* Correspondence: Ç. Akçay, Department of Biological Sciences, Virginia Tech, Blacksburg, VA 24061, U.S.A.
E-mail address: akcay.caglar@gmail.com (Ç. Akçay).

http://dx.doi.org/10.1016/j.anbehav.2017.05.026
0003-3472/

with song sparrows, *Melospiza melodia*, living in Washington, U.S.A. (Beecher, 2017). In this population, song learning occurs in the period after natal dispersal and before the bird's first breeding season the following spring. Neighbours typically 'share' song types, and this song sharing has been shown to be a result of song learning (Beecher, 2008; Beecher, Campbell, & Stoddard, 1994; Nordby, Campbell, & Beecher, 1999). The period of song learning also coincides with territory establishment during which young birds also engage in aggressive interactions with their future neighbours (Arcese, 1989; Nice, 1943), and shared songs are used by adult birds as part of a graded signalling system in aggressive interactions (Akçay, Tom, Campbell, & Beecher, 2013; Burt, Campbell, & Beecher, 2001). All of these lines of evidence suggest that song learning may be influenced by the amount of aggressive and competitive interactions between the tutors and the young birds. We term this hypothesis the 'competition' hypothesis.

A different line of thinking, however, suggests that even under these circumstances the songbird tutor–tutee relationship could be an at least partially cooperative one. As has been shown for numerous diverse taxa, territorial neighbours often enter into a 'dear enemy' relationship where they are more tolerant of their neighbours than they are of strangers (Akçay et al., 2009; Fisher, 1954; Temeles, 1994). Hence it is possible that it might actually benefit an established territorial adult to 'teach' his songs to a young bird who is in a position to become his future neighbour; in short, a 'dear tutor–tutee' relationship could underlie and support a 'dear enemy' relationship. This idea can be seen as an extension of the observation that in many group-living species with vocal learning (e.g. dolphins, parrots and cooperatively breeding songbirds), vocal learning seems to have an affiliative function in which individuals learn their vocalizations from members of their social groups (Akçay, Hambury, Arnold, Nevins, & Dickinson, 2014; Berg, Delgado, Cortopassi, Beissinger, & Bradbury, 2012; Brown, Farabaugh, & Veltman, 1988; Price, 1998; Sharp, McGowan, Wood, & Hatchwell, 2005). This 'cooperation' hypothesis is also consistent with recent reviews of animal 'teaching' in which the putative tutor does not obtain immediate benefits (and may even pay immediate costs) by engaging in the teaching of a tutee (Hoppitt et al., 2008). Under this view, older birds would reap some form of delayed benefit from tutoring young birds and having them as neighbours. This benefit might come in the form of increased breeding success (Beletsky & Orians, 1989), access to extrapair females that are mated to the young males, or less competition for within-pair paternity from these young males (Hill, Akçay, Campbell, & Beecher, 2011). The last two potential benefits are based upon the findings that in many songbirds, including song sparrows, the older males are more likely to pursue extrapair matings successfully (Akçay et al., 2012; Hill et al., 2011; Hsu, Schroeder, Winney, Burke, & Nakagawa, 2015).

Here we present a test of competition and cooperation hypotheses in song sparrows. Song sparrows are close-ended learners who learn their songs in the period after dispersal from the natal area and the beginning of their first breeding season the following spring and do not change their song repertoire in subsequent years (Nordby, Campbell, & Beecher, 2002). Extensive field studies have shown that while on average a bird copies about half of his eight or nine songs from a single tutor (the best tutor) and the rest from multiple other tutors, there is a range of learning strategies, varying from copying all songs from a single tutor to copying a single song from each of eight or nine tutors (Akçay, Campbell, Reed, & Beecher, 2014; Beecher et al., 1994; Nordby, Campbell, & Beecher, 2007; Nordby et al., 1999). As noted above, adult song sparrows use shared songs as part of a graded signalling system that may indicate the primary role of competitive interactions in song learning. At the same time, multiple studies have shown that male song sparrows can individually recognize their neighbours and generally show reduced aggression to neighbours compared to strangers (Akçay, Reed, Campbell, Templeton, & Beecher, 2010; Akçay et al., 2009; Wilson & Vehrencamp, 2001), suggesting that the opportunity for cooperative interactions with potential tutors exists.

We tested the two hypotheses by asking whether a bird would respond more or less aggressively to a simulated intrusion by a former tutor compared to a stranger, and whether aggressive response would vary with how much the young bird had learned from the tutor. Specifically, in a playback experiment to subjects with known song-learning histories, we compared their aggressive response to the tutor from whom they had learned the most, to their aggressive response to songs from a stranger. The cooperation hypothesis predicts that tutees should respond less aggressively to their best tutors than to strangers, and less aggressively to tutors from whom they learned more than from tutors from whom they learned less. In contrast, the competition hypothesis predicts precisely the opposite: subjects should respond more aggressively to their best tutors than to strangers, and more aggressively to tutors from whom they learned more than to tutors from whom they learned less.

METHODS

Study Site and Subjects

We studied a banded population of song sparrows in Discovery Park, Seattle, Washington, U.S.A. Between 2009 and 2014 all the territorial males (about ~120 males each year) were banded with a U.S. Fish and Wildlife Service metal leg band and three coloured leg bands. As a part of our long-term study on song learning (Beecher, 2008), the complete song repertoire of each male was also recorded with Marantz PMD 660 recorders and Sennheiser ME66/K6 shotgun microphones. The full repertoire was considered to be recorded after at least 16 song switches (Nordby et al., 1999). Subjects in the playback experiment were 13 banded male song sparrows from our study population in Discovery Park whose songs had been recorded. We tested each subject twice on different days with a counterbalanced order for two trial types. The experiments were conducted from 18 March to 14 April 2014.

Tracing Song Learning

We chose males of known age and song-learning history that held territories in the spring 2014. Three of the subjects hatched in 2009, six in 2010 and seven in 2011. All the subjects were banded either before their first moult (juvenile plumage) or while singing plastic song before their first spring when the songs crystallize (around 1 March). We made sonograms of all the songs in the repertoire of the tutees and potential tutors using Syrinx (www.syrinxpc.com, John Burt, Seattle, WA). We printed out several variations of each song of all the males. The tutors for each tutee were determined as described in detail in our previous studies (Akçay, Campbell, Reed, et al., 2014; Nordby et al., 1999). Three judges visually compared the songs of the tutees and tutors independently and laid out matching songs on a large table. After this step, the three judges discussed their best match decisions, and arrived at a consensus. If a single adult had the best matching song for a given tutee song, that tutor got a credit of 1 for that song. If more than one adult had equivalently good matches for a given tutee song, then each tutor got credit of $1/N$, where N was the number of tutors with equally good matching songs. Because of the high level of song sharing in our population (Hill, Campbell, Nordby, Burt, & Beecher, 1999), splitting credit between multiple tutors happens about half the time (Akçay, Campbell, Reed, et al., 2014).