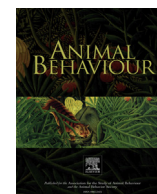




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Birdsong learning as a social process

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This paper describes a 30-year investigation into the role of social and ecological factors affecting song learning in song sparrows, *Melospiza melodia*. It addresses the question of why song sparrows learn the songs they do, given that they are exposed to many more songs than they will keep for their final repertoire of 7–11 song types. A young song sparrow moves from his natal area at about 1 month of age, eventually settling in an area where he learns the songs of the resident males and attempts to establish his own territory. Birds that share many songs with their neighbours in their first breeding season (the spring following their hatch summer) survive for more years on territory than birds that do not. Many features of the song-learning process lead to a high level of sharing with first-year neighbours, including preferentially learning the songs of their tutor-neighbours who survive the winter, and learning songs that are shared by several tutors. Social interaction appears to be critical in song learning, but indirect effects (eavesdropping on adults countersinging) seem to be at least as important as direct interaction between the young bird and his tutor-neighbours. Although our evidence suggests that the song-learning strategy of young song sparrows is beneficial to them, a preliminary analysis suggests it may not benefit their tutors.

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Song is a common form of communication in a wide variety of animal groups (Searcy & Andersson, 1986). Song in the oscine passerines (songbirds) is of special interest because it is learned. Vocal learning has evolved in only three groups of birds (songbirds, parrots and hummingbirds) and a small number of mammals (Jarvis, 2004), including of course humans. The songbirds are particularly interesting because of the amazing variety of song-learning patterns that have been discovered within this group of 4000+ species (Beecher & Brenowitz, 2005; Kroodsmas, 1988, 1996). Because song is learned in songbirds, songbirds can be used to address a series of questions about vocal learning. Of the many songs heard by a young bird, which does he learn, which does he reject, and why? Whom should the bird learn from? Do song learners benefit from their learning strategy? Do song tutors benefit from being copied? In this paper I describe a research programme that addresses these and related questions, and which thereby provides an unusual opportunity to examine the function of vocal learning.

In most songbirds, song functions in intrasexual competition and mate attraction. While this paper focuses on cases where only

males sing, singing by both sexes appears to be the ancestral condition in songbirds, and is common in tropical and nonmigratory species generally (see recent reviews by Logue & Hall, 2014; Odom, Hall, Riebel, Omland, & Langmore, 2014). In most territorial temperate-zone passerines, only males sing, and the major intra-sexual context is 'posting' the territory with long-distance song and communicating with neighbours to negotiate territorial boundaries (review in Catchpole & Slater, 2008).

The study of song learning in the laboratory was pioneered by Peter Marler (e.g. 1970), who realized that the ultimate in experimental control of acoustic and timing variables could be achieved by isolating the song learner and delivering tutor song via tape recorder (later, computers). From this experimental paradigm came many important generalizations about song learning, including the concept of the sensitive period for song memorization, and the species-specific stimulus filtering mechanism for species song (often referred to as the 'innate template'). In what has become established as the prototypical, textbook example, Marler (1970) showed that a white-crowned sparrow, *Zonotrichia leucophrys*, male will develop normal song only if he hears conspecific song during an early sensitive period (roughly the second month of life). Moreover, the bird will reject heterospecific song heard during this period, as well as conspecific song heard after the sensitive period. The tape tutor paradigm that Marler developed has been

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particularly valuable in identifying the sensory mechanisms that guide and constrain song learning (e.g. Soha & Marler, 2000, 2001).

Although they are sometimes overlooked in discussions of avian song learning, striking differences between the song-learning programmes of different passerine species have been revealed in comparative studies (Beecher & Brenowitz, 2005; Kroodsma, 1978, 1983; Marler & Peters, 1988a; Nelson, 1999; Slater, 2003). Key differences include how long the sensitive period stays open (in some cases throughout life), how many songs the bird keeps for his final repertoire (ranging from one to over a hundred), whether the bird imitates tutor songs or improvises or invents new songs, whether the bird requires early exposure to conspecific song, and how constrained the bird is to copy only songs that fit species-specific parameters (Beecher & Brenowitz, 2005).

Despite years of intensive study, however, there is a major lacuna in the study of birdsong: we know virtually nothing about the function of song learning. Presumably, song learning evolved in the oscine passerine lineage because of advantages it conferred on the song learner. Yet exactly what are these advantages? They have not been identified for a single species to date.

The likely explanation for this gap in our knowledge is the difficulty of studying song learning under natural conditions. Hints that it is necessary to consider song learning in its natural context came first from experiments showing that birds learn more readily from live tutors than from tape-recorded song (Baptista & Petrinovich, 1984; Chaiken, Bohner, & Marler, 1993; Clayton & Pröve, 1989; Cunningham & Baker, 1983; Kroodsma & Pickert, 1984a, 1984b; Kroodsma & Verner, 1978; Nicolai, 1959; Payne, 1981; Price, 1979; Rice & Thompson, 1968; Thielke, 1970; Waser & Marler, 1977). Moreover, some of the rules of song learning derived from tape tutor studies bend, if not break, when the song tutors are actual birds. For example, whereas tape tutor studies had indicated that the sensitive period for white-crowned sparrows closes at approximately 50 days of age, and that heterospecific songs are uniformly rejected (Marler, 1970), Baptista and Petrinovich (1984, 1986) showed that if a young white-crowned sparrow was exposed to a tape tutor through 50 days of age and thereafter exposed to a live tutor, the young bird would learn the song of the live tutor, and in some cases would do so even if the tutor was a heterospecific.

Although differences between song learning from tape tutors and song learning from live tutors have been the subject of considerable debate (Baptista & Gaunt, 1997; Nelson, 1997, 1998), there is consensus on one major point, which is that a live adult singer is a more potent stimulus during song development than are songs presented through loudspeakers alone (e.g. Casey & Baker, 1993). But at the same time, it is unclear if this difference can be extrapolated to real-world contexts in any simple way. As Marler and Peters (1988b) noted, both the 'tape tutor' and 'live tutor' experimental set-ups are 'unnatural'. The tape tutor design can be extrapolated to the real world if in nature a young bird learns his songs by listening to an adult bird singing solo and out of sight. In contrast, the laboratory live tutor design assumes that the young bird normally learns from a song tutor who is up close and interactive. Neither may be true. This simple observation leads to the conclusion that the function of song learning must be studied under natural conditions, in the field. Laboratory experiments, with their greater experimental control, still have a place in this search; particularly 'seminatural' ones that are carried out in a way that captures key features of the natural social environment. And needless to say, these seminatural laboratory studies require prior field studies that identify likely candidates for these 'key features of the natural environment'.

In this paper I describe a case study of our 30-year research programme attempting to identify the key social factors in song

learning in the song sparrow, *Melospiza melodia*. Other research efforts that have pursued this same goal include Kroodsma (1974) on Bewick's wrens, *Thryomanes bewickii*, Jenkins (1978) on saddlebacks, *Philesturnus carunculatus*, Payne (1983) on indigo buntings, *Passerina cyanea*, Bell, Trail, and Baptista (1998) on white-crowned sparrows, Liu and Kroodsma (2006) on chipping sparrows, *Spizella passerina*, and Nelson and Poesel (2009) on white-crowned sparrows. Generally these studies have shown that after natal dispersal, young birds learn the songs of their future territorial neighbours. But because young birds learn only a subset of the songs they hear (sometimes only a single song), the crucial question becomes: why do they learn (retain) the particular songs they do as opposed to others to which they were exposed?

BACKGROUND AND METHODS

The song sparrow is a common species found throughout North America. Song sparrows have the most genetically distinct populations of any bird in North America. We are studying a subspecies (*M. m. morphna*) found in the Pacific Northwest. The total number of subspecies of song sparrow is much debated, but the most recent study puts the number at 25 (Patten & Pruett, 2009). This context must be kept in mind, since, as will be discussed later, there may be significant biological differences between the song-learning programmes of some of these different subspecies.

Our study population is a sedentary (nonmigratory) population of song sparrows in an undeveloped 534-acre park in Seattle, Washington, U.S.A. Although the park has some of the characteristics of an island, being bounded on the north by Puget Sound, its other boundaries are with residential areas, generally hospitable to song sparrows, if less so than the park. Song sparrows in this population are year-round resident on their territories, although they are fully territorial only in and around the breeding season, which is roughly March through July. Birds sometimes make small lateral moves if an adjacent territory opens up, but otherwise are strictly sedentary.

Song sparrows in this population typically have 7–11 distinct song types. Most often they will share some but not all of their songs with one neighbour, a somewhat different set of songs with a second neighbour, and so on. An example is shown in Fig. 1. This pattern of song sharing has been observed in other Washington populations (Cassidy, 1993; Hill, Campbell, Nordby, Burt, & Beecher, 1999; Reeves & Beecher, n.d.) and in a California population (Wilson, Towner, & Vehrencamp, 2000), but it is not found in the eastern subspecies, *M. m. melodia* (Hughes, Anderson, Searcy, Bottensek, & Nowicki, 2007). We consider this interesting population difference later.

Song sparrows are age-limited song learners: they do not modify their song repertoires after their first year of life (Nordby, Campbell, & Beecher, 2002). A laboratory study using tape-recorded song as tutor song showed that eastern song sparrows learn most of their songs during a sensitive period spanning roughly the second and third months of life (Marler & Peters, 1987). However, tape tutor studies can underestimate the sensitive period, and moreover eastern subspecies of song sparrows may have a very different song-learning programme from western subspecies (see Discussion). On the basis of field studies of our western song sparrow population, we have established that song learning continues into the bird's first spring, and is completed by the time he is 9–10 months old. Some of this late learning may occur in late summer or autumn of the natal year, but our laboratory and field studies have indicated that the primary effect occurs later, early in the following spring (January, February and early March for our birds). Although some of our laboratory studies have indicated that birds in our population are capable of

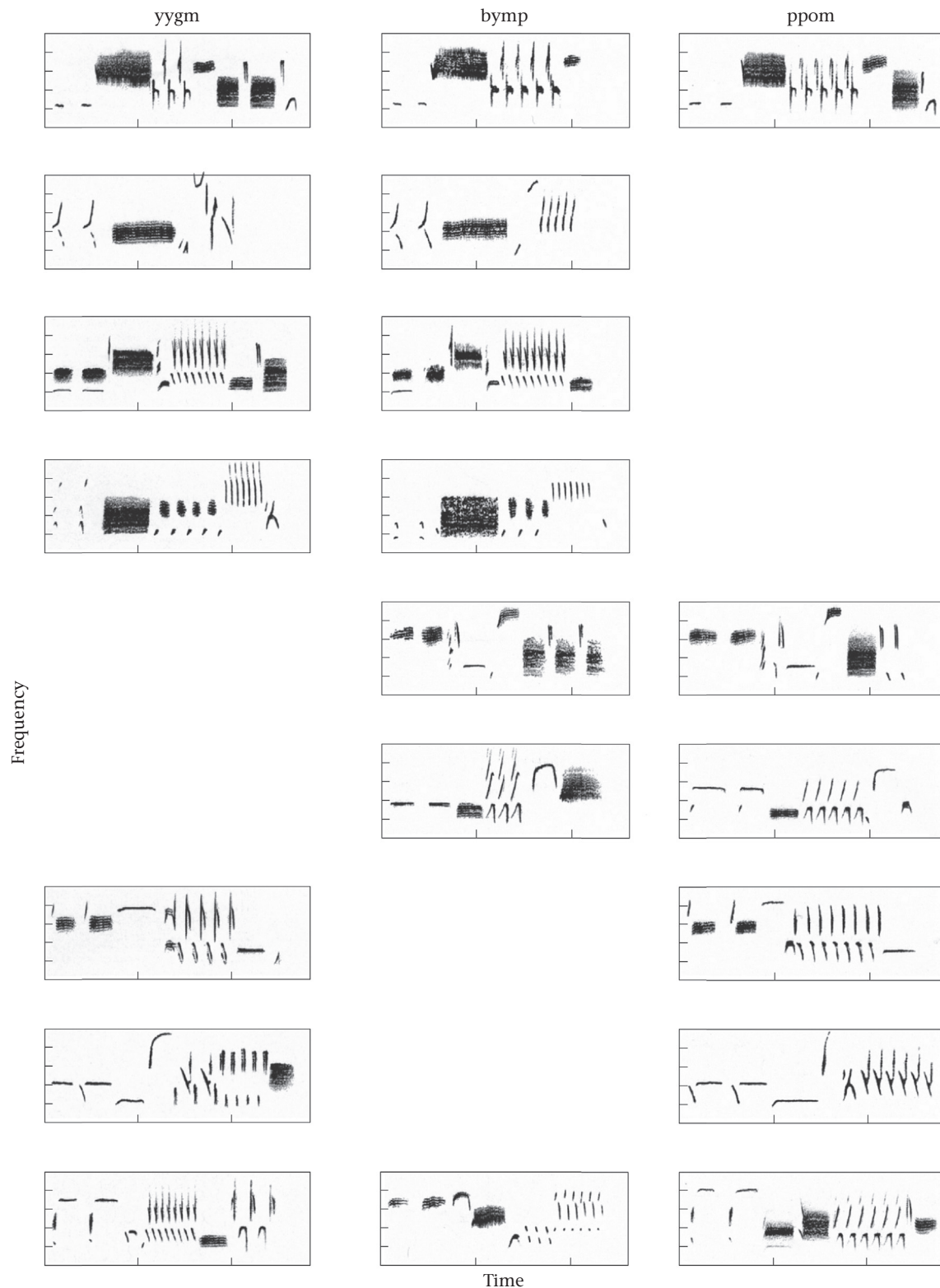


Figure 1. Partial repertoires of three neighbouring song sparrows: yygm, bymp and ppom. Each row shows shared songs except for the bottom row, which shows three unshared songs. To be considered shared, two songs had to match at least half of their component phrases. In borderline cases, we put more weight on the more invariant early portions of the song and less on later parts of the song. The number of elements in the phrase was generally disregarded, as this is a feature that the bird often varies from one rendition to another (e.g. fourth shared song, middle phrase, following the buzz: in these renditions, yygm has five elements, bymp has three elements, but the phrase is considered the same because the component elements are the same). A borderline case of sharing is the sixth shared song: the two songs differ in terms of the initial paired elements and the end phrase. The middle three phrases (buzz, trill and high sweep) are the same, so the song is considered more than half similar. Frequency scale 0–10 kHz, markers at 2 kHz intervals, time marker 1 s. Reprinted from Figure 1 in [Beecher, Campbell, & Nordby \(2000\)](#).

de novo learning of new song types in their first spring (Nordby, Campbell, & Beecher, 2001; Nulty et al., 2010; Templeton, Burt, et al., 2012a), in our field studies we cannot tell whether this late learning consists of memorization of new songs de novo or preferential retention of songs heard and memorized earlier, in the natal summer (Nelson & Marler, 1994). This ambiguity exists because in our resident population, an adult singer in the spring will have also been present in the population the previous summer. In this paper I focus on the adaptive value of this late learning, and from the functional point of view, it is not really critical whether late learning/influence is de novo (i.e. the songs are heard for the first time), or is simply reinforcing earlier song exposure.

In hopes of identifying the key social variables in song learning for our study species, we began our investigations in the field (Beecher, Campbell, & Stoddard, 1994; Nordby, Campbell, & Beecher, 1999). While song sparrows continue to modify their repertoire (dropping songs, rearranging elements, perhaps learning new songs) into their first spring (Nordby, Campbell, & Beecher, 2007), they do not change their song repertoires after their first breeding season (Nordby et al., 2002). Given these facts, we reasoned that if we colour-banded and recorded all (or nearly all) of the adult males in this population, we would then be able to identify the song tutors of all young birds entering the population in that year, provided of course that the young birds learned their

songs after natal dispersal. Postdispersal learning is the typical pattern in songbirds (see review in Beecher et al., 1997). In our population, birds that we banded in the nest and subsequently recaptured postdispersal sang song types of their postdispersal area rather than of their natal area.

Typically 100–150 song sparrow males are on territories in our study population in a given year. After a preliminary study with birds hatched during 1986–1990 (Beecher et al., 1994), we carried out full-scale studies of cohorts of young birds who immigrated into our study site in four hatch years: 1992 (Nordby et al., 1999), 2009 (Akçay, Reed, Campbell, & Beecher, 2014), 2011 and 2012 (Akçay, Campbell, & Beecher, n.d.). We considered as possible song tutors all older birds in the study population that were on territory in the subject's hatching year. We identified the older bird with the most similar rendition of the song type (complete with idiosyncratic features not seen in other renditions of the type) as the young bird's 'probable tutor' for that type. This judgement is rarely problematic, because song sparrow songs are complex and similar songs stand out on the background of the seemingly infinite variety of possible song types. When two (or more) older birds had versions of a song that were highly similar to the young bird's – not unusual in this population where neighbours share songs – they would both receive credit as the tutor for that song. See Fig. 2 for an example, and Beecher (2008) for a detailed discussion of our methodology.

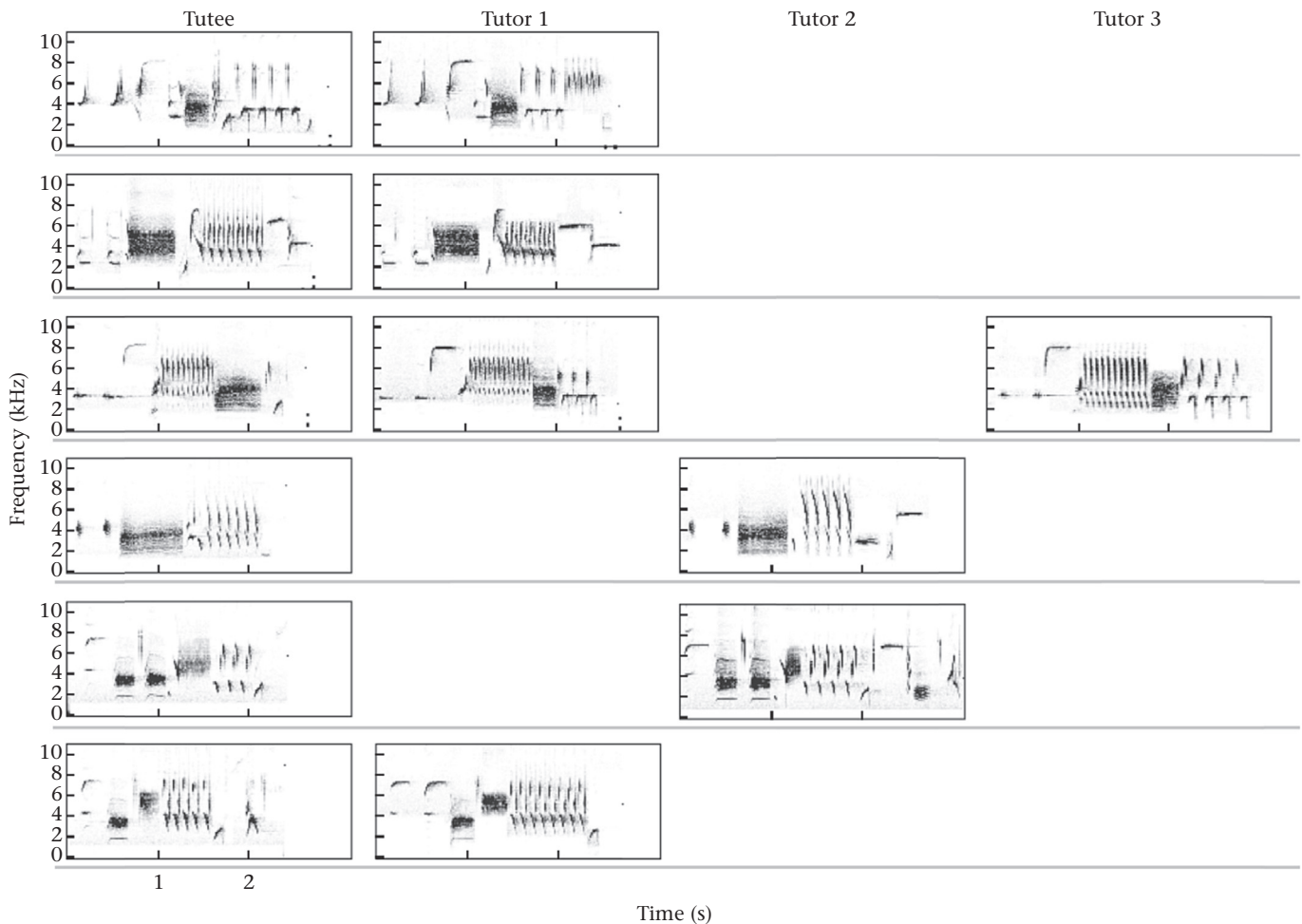


Figure 2. An example of song learning from multiple tutors. A partial repertoire of a tutee (five out of his nine songs), with three out of five matching tutors. The bottom two rows show two major variations of the same song type that the tutee had in his repertoire. For this variation, tutor 1 and tutor 2 each shared 0.5 credit, as one of the major variations matched tutor 1, whereas the other matched tutor 2. Reprinted from Figure 1 in Akçay, Reed, et al. (2014).

In the case of western song sparrows, because they copy their complex songs rather precisely (in our laboratory studies as well as in our field studies), it is relatively easy to find good matches of tutor-to-tutee songs. In 4 years (1992, 2009, 2011, 2012) we studied cohorts of 30–40 young birds that had dispersed into the study site, with approximately 120 adult potential song tutors. In all 4 years, we were able to find good matches for at least 95% of their songs. The few songs that we were unable to match to tutor songs may have been copied from other birds on the periphery of the song area (or from the one small area within our study area housing a military installation that we could not access); most such ‘mystery’ songs were found from birds in these tricky areas. The alternative is that these few songs were improvised. In any case, these unidentified songs have not been included in any of our analyses. And as alluded to above, on a number of occasions, birds that we had banded in the nest subsequently dispersed within the study site. In all of these cases, the young bird copied songs of his postdispersal neighbours and no songs of his father.

SONG LEARNING IN WESTERN SONG SPARROWS

By a combination of field and laboratory studies, we have tried to characterize the song-learning strategy of song sparrows in our population. Note that in the following I use the word ‘tutor’ merely to designate an older bird from whom the young bird has learned songs (or could have potentially learned songs). The use of this term is not meant to imply that the tutor intended to teach the young bird songs, or that he benefited in some way by doing so. The focus here is primarily on the young bird, and the goal was to characterize each male’s song-learning ‘strategy’, a term implying that the male indeed gains by learning the particular songs that he does, and in the way that he does. Whether or not the older bird, the ‘tutor’, gains is another question altogether, and, as we will see, a more difficult one to answer. I will present the evidence we do have on this question, and suggest future avenues of research.

Young Birds Learn Songs of Multiple Adult ‘Tutors’ (Usually 3–5)

Our preliminary study (Beecher et al., 1994) and our four subsequent full-cohort studies consistently indicated that a young song sparrow learns his 7–11 songs from several different adults tutors, most often three to five of them (Fig. 2) (from Akçay, Reed, et al., 2014). As will be discussed below, however, young birds vary from cases where all or most of their songs are learned from one tutor, to cases where they learn no more than one or two songs from a given tutor.

Song Learning and Territory Establishment Strategies Are Correlated

Typically, a bird’s song tutors are its neighbours during its hatching summer, and, if those neighbours survive the winter, they will also be the young bird’s tutors the following spring (during the young bird’s first breeding season), suggesting that the young bird moves around in a fairly restricted area while he is learning his songs. The young bird usually establishes his territory within the territorial range of his song tutors, sometimes replacing a tutor who has died. The young bird typically learns the most from and settles closest to one of the surviving tutor-neighbours. It appears that in the rare cases when the young bird settles away from his song tutors, this is because no vacancies opened up in the area (i.e. all the tutors survived the winter).

The correlation between a young bird’s song-learning strategy and its territory establishment strategy is diagrammed in Fig. 3. There is considerable variation, which cannot be indicated in this diagram, as some young birds will become semiterritorial as early as late summer or early autumn, while others will do not do so until the following spring. This variation may be correlated with hatch dates of the young birds, which can range from early May to early July, but we cannot determine this since we catch and band the young birds only after they have dispersed into the study area (although we have banded birds in the nest, most of them disperse out of the study area).

Young Birds Preferentially Learn Tutor-shared Songs

As noted earlier, in our field population, neighbours typically share a portion of their song repertoires, on average about two to four per neighbour out of their 7–11 song types. We have found that a young bird preferentially learns (or retains) song types shared by two or more of his tutors (Beecher et al., 1994); an example is shown in Fig. 4. There are several possible reasons that shared song types might be particularly salient, including: (1) they are heard more than unshared song types; (2) ‘the same song’ is being sung by several birds; or (3) they are heard more often in countersinging interactions than are unshared songs. While the first possibility is purely an acoustical or dosage issue, the second and third possibilities identify social factors and are consistent with a ‘bet-hedging’ strategy that guarantees that the young bird has song types he will share with his neighbours in his first breeding season. If instead the bird learned tutor-unique songs, he would have songs ‘specialized’ for these particular tutor-neighbours (i.e. share these songs with one neighbour only), but these would be good only until the tutor dies, whereas a shared song is good until

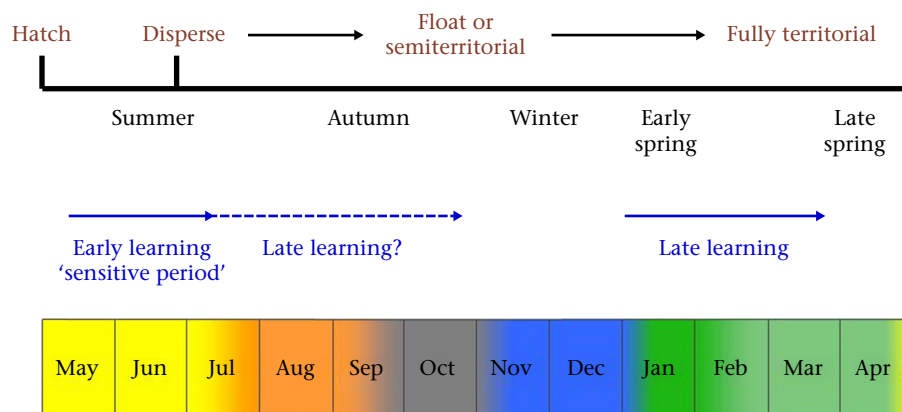


Figure 3. Correlation of song learning and territory establishment in western song sparrows. Most birds hatch in late April, May or June and disperse about 1 month later. Young birds vary considerably as to when they begin acting territorial, the earliest being in August, the latest being in January or February. Our evidence suggests that most learning (or late influence) happens in January and February, but some may occur in the autumn as well.

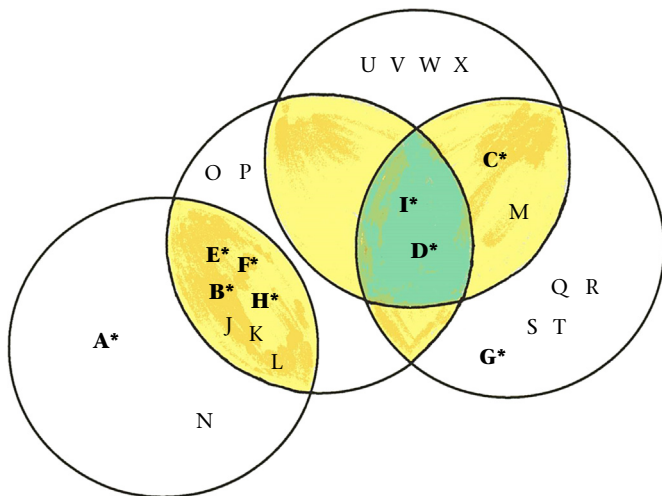


Figure 4. Subject abgm learned songs from four older birds (circles). These tutors had a total of 24 song types (uppercase letters), 13 of which were unique or unshared, and 11 of which were shared across tutors (nine songs were shared by two tutors, and two songs were shared by three tutors). The young bird retained for his final repertoire 7 of the 11 shared song types but only 2 of the 13 unshared (unique) song types of these tutors; the songs he learned are shown in bold and marked with an asterisk.

all the birds having it in the neighbourhood die, and probably even longer because other young birds moving into the area would also be preferentially learning shared types.

Young Birds Learn/Retain More from Tutors That Survive the Winter

Young song sparrows learn (or retain) more songs from older birds that survive into the new year than they do from those that do not survive (Akçay, Reed, et al., 2014; Nordby et al., 1999). This most likely reflects interactions between the younger bird and his tutors in the early spring (January, February and early March). This finding has been replicated in our three subsequent studies of age cohorts, and also in laboratory studies described below.

Young Birds 'Individualize' Their Song Repertoires

Although a young song sparrow in this population learns the songs he will share with his neighbours in his first breeding season, there is one important exception to that rule (Nordby et al., 2007). In the transition from plastic song (heard in the autumn but especially in January and February) to final crystallized song (generally February or March), the young bird often alters a song so that it becomes a poorer match to the model song of the putative tutor and to similar songs of his present neighbours. The bird 'individualizes' his version of the song type by rearranging the order of elements of the original song, or slightly modifying one element, or substituting one similar element for another. The song may still be perceived by the birds as a shared song (even if it perhaps no longer meets our criteria for sharing), while perhaps at the same time being perceived as that bird's particular version of the song type. Thus the bird gets to have songs that functionally are both shared with his neighbours yet unique to him.

Young Birds Benefit from Having Songs They Share with Their First-year Neighbours

Our field evidence suggests that young song sparrows benefit by beginning their first breeding season sharing songs with their neighbours. In a study of 45 young birds (hatch years 1990–1993) in our population (Beecher, Campbell, & Nordby, 2000), we found

that the number of years that birds survive on territory is positively correlated with the number of songs that they shared with their neighbours in their first breeding season (Fig. 5), but not with the total number of songs in their repertoire. A similar survival-sharing correlation has been found in a California song sparrow population (Wilson et al., 2000).

Laboratory Experiments: The Importance of Social Interaction in Song Learning

Our field studies set the stage for several 'seminatural' laboratory studies, in which we retained some of the key features of the natural world – including multiple live tutors singing from spatially separated 'territories' – while we maintained some degree of experimental control (e.g. we could control where the young subjects were relative to particular tutors, when particular tutors were present, and so forth). We carried out two of these studies in aviaries on the roof of our laboratory building, in an arrangement designed to resemble natural field conditions (Nordby et al., 2001; Nordby, Campbell, Burt, & Beecher, 2000). In both of them, we used four adult males who had been neighbours at our study 12 km away. They shared some of their songs, and when we stationed them on 'territories' (small aviaries containing a potted tree and numerous additional perches) on the four corners of the roof, they did in fact become quite territorial and countersang with one another like song sparrows in the field. In both experiments, young birds were moved from territory to territory, similar to the way they move in the field (Arcese, 1987, 1989; Templeton, Reed, Campbell, & Beecher, 2012).

In our first experiment (Nordby et al., 2000), eight hand-raised song sparrows were moved from one tutor to another every few days in June and July, so that they got to see and hear each of the four tutors up close one-quarter of the time and hear them at a distance three-quarters of the time. In the autumn and the following spring, the young birds were split into one of two

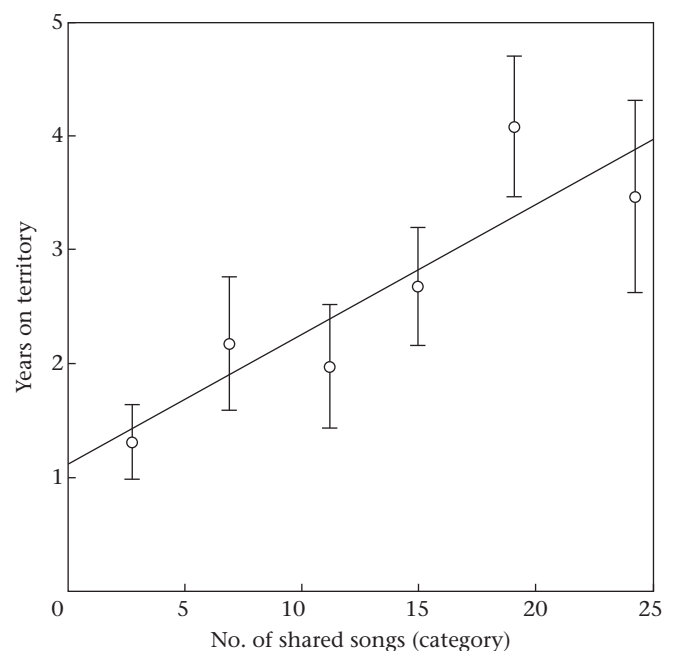


Figure 5. Years survived on territory as a function of number of shared songs each bird had in its first breeding season. Categories of shared songs are 1–4 ($N=3$), 5–8 ($N=5$), 9–12 ($N=10$), 13–16 ($N=10$), 17–20 ($N=9$) and 21–31 ($N=8$). Mean sharing in each of the six categories is 2.67, 6.8, 11.1, 14.9, 19.0 and 24.2. Reprinted from Figure 2a in Beecher, Campbell, & Nordby (2000).

experimental conditions. Subjects in the 'stationary' group were always next to a particular one of the four tutors. Subjects in the 'rotator' group spent equal time next to each of the four tutors.

Although all subjects learned from multiple tutors, usually from three or all four tutors, subjects who were next to just one of the tutors in the late phase preferentially retained songs of that tutor for their final repertoire, while subjects who continued to rotate between tutors in the late phase all learned the most from one particular tutor of the four; this tutor sang the most of the four tutors (Table 1). That the most popular tutor for the rotating subjects was not the most popular tutor overall for the 'stationary' subjects indicates that the proximity effect trumped the tutor effect (whether the latter was a dosage effect or something else).

In our second seminatural experiment, we used the same basic layout on the roof, again with four (new) adult tutors who shared some songs with one another, each stationed in one corner of the roof (Nordby et al., 2001). We again rotated the young birds among these tutors during June and July (phase 1). After the birds had approximately 2 months off (August and September), we replaced two of the original tutors with two new tutors for a second period of song exposure (phase 2). Thus, there were six tutors from whom the young birds could learn songs: two 'permanent' (present in both phases), two 'early-only' (phase 1 only) and two 'late-only' (phase 2 only). The two 'late-only' tutors shared one song with each other but no songs with the two 'early-only' tutors or the two 'permanent' tutors. In the second phase, the young birds were stationed next to one of the four tutors.

Fig. 6 shows the results of this experiment superimposed on a diagram of the experimental design. These results differed in several important ways from those of the first experiment. Virtually no songs of the two early-only tutors were retained. One of the late-only tutors was the most effective tutor, with over half of all songs learned by the subjects traced to him. The effectiveness of the late-only tutor occurred in the face of what we had thought would be two severe handicaps: a late start (29 September), which is well past the end of classical critical period (the young birds were now 140 days old) and his never being close and visible to three-quarters of the subjects (they were stationed next to one of the

other tutors). Thus, in this experiment, the tutor effect (whatever it was) trumped the proximity effect.

Besides reaffirming the importance of late learning, this second study made two additional points. First, it showed that song learning requires neither proximity nor visual contact. Second, it suggested that auditory interaction may play a critical role in song learning. Song tutors were recorded for 1 h per day, and we observed that our supertutor was extremely interactive with other tutors, and perhaps with the young birds as well (our recordings were inadequate on the latter point). These observations were crucial to the design of our subsequent experiments.

Singing Interactions, Both Direct and Indirect, Are Critical

In a third seminatural experiment (Beecher, Burt, O'Loughlen, Templeton, & Campbell, 2007), we exposed hand-raised song sparrows to four adult tutors in May and June (early). In January, February and March (late) they were exposed to only two of those tutors, one in close visual contact, and the other was unseen but overheard interacting with another young bird. As expected from previous studies, the subjects learned more from the tutors they experienced late as well as early than they did from tutors they experienced only early. However, subjects learned more from the tutor they overheard interacting with another young bird than they did from the tutor they saw and interacted with vocally. Subjects learned relatively more from the interactive tutor when there was a blind between them, suggesting that the up-close and personal nature of the direct interaction was somewhat inhibitory. These results provide the first evidence that young birds choose their songs by eavesdropping on interactions, and in some cases may learn more by eavesdropping than by direct interaction. It also again demonstrates that visual contact is not essential for song learning.

In a similar study (Burt, O'Loughlen, Templeton, Campbell, & Beecher, 2007), we exposed hand-raised song sparrows sequentially to two pairs of live tutors (A always with B, C always with D) in May and June (early), then in January, February and March (late) to computer presentation of songs from two of the original tutors ('virtual tutors' A and C), one of which sang interactively with the young bird, and the other of which sang asynchronously. Subjects learned more from the interactive virtual tutor (e.g. tutor A) and also retained more songs from the early partner of the interactive tutor (tutor B) than they did from the noninteractive tutor (tutor C) or his early partner (tutor D). In fact they actually retained more songs from the early-only partner of the interactive tutor (B) than from the late interactive tutor (A). These findings indicate that not only is the bird more likely to learn songs from an interactive tutor, but he is also more likely to retain songs for his final repertoire that he heard early used as *replies* to the interactive tutor. Again, this result points to the important role of eavesdropping on singing interactions for song learning.

The role of overheard social interaction was also revealed in a field experiment (Templeton, Akçay, Campbell, & Beecher, 2009). To test the hypothesis that eavesdropping on singing interactions of adults is a key social event in song learning, we compared the response of radiotagged juvenile song sparrows to simulated adult countersinging versus simulated solo singing during the midsummer sensitive period. Juveniles approached the simulated interactive singing of two song sparrows but not the simulated solo singing of a single song sparrow, which they treated similarly to heterospecific singing (a control condition). These results indicate that during the prime song-learning phase, juvenile song sparrows are attracted to singing interactions between adults, but not to singing by a single bird, and they suggest that singing interactions may be particularly powerful song-tutoring events.

In another field experiment (Templeton, Campbell, & Beecher, 2012), we examined how adult male song sparrows

Table 1

Number of song types that a tutor, or another young bird in the cohort, matched with the subject, devalued by the number of other tutors identified for those song types

| | Tutor scores | | | | Cohort |
|-------------------|--------------|-------------|------------|-------------|------------|
| | T1 | T2 | T3 | T4 | |
| Stationary | | | | | |
| AY | 2.5 | 1.75 | — | 1.25 | 0.5 |
| RP | 1 | 5.25 | — | 0.25 | 0.5 |
| RI | — | — | 1.5 | 1 | 1.5 |
| BY | 0.33 | 1.33 | 1.5 | 2.33 | 0.5 |
| Rotated | | | | | |
| BP | 2.5 | 0.5 | 1 | — | — |
| BR | 1.5 | — | 1 | — | 0.5 |
| RG | 1.5 | 0.5 | 1 | — | — |
| RY | 4.5 | — | 0.5 | — | 1 |

Cohort tutor score refers to songs that were either more like those of another young bird in the cohort than they were like the tutor song, or more like another cohort's song in one respect and more like the tutor's in another (in which case credit was shared). Cohort shares were possible because four of the young birds were present simultaneously, each one next to one of the four tutors, and so each could hear one another singing (at a distance) in this late tutoring phase (winter/spring). In the stationary group, a bird was always stationed next to the same tutor, whereas in the rotated group, a bird was stationed next to one tutor for 1 day, then stationed next to another tutor for 1 day, and so on. Each group was exposed to tutors for 1 day and then in isolation for 2 days. The high tutor score for each bird is shown in bold, while the adjacent tutor (stationary group only) is indicated in italics. The probability of obtaining this exact pattern of primary tutor influence for the stationary subjects was 1 in 256, or $P = 0.004$ (data from Nordby et al., 2000).

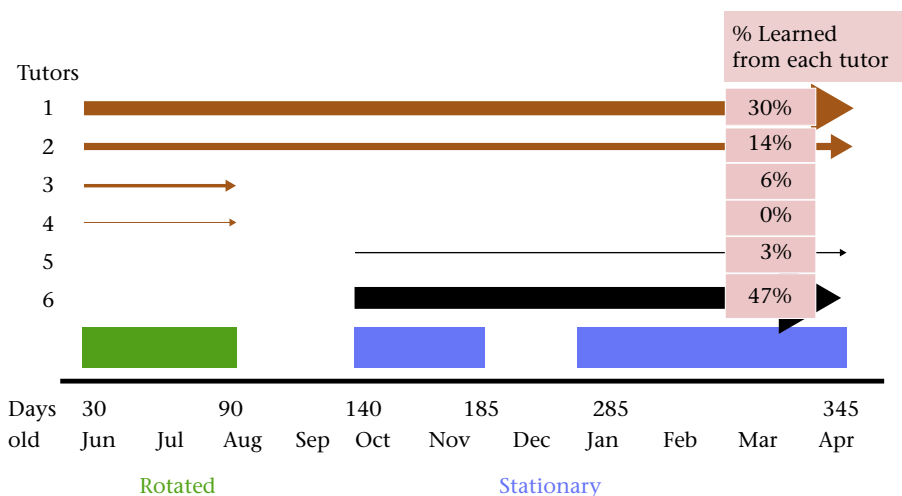


Figure 6. Experimental design. During the early phase 1 (7 June – 18 August), all subjects were rotated equally between four tutors T1–T4. During the late phase 2 (29 September – 13 November), subjects were stationed next to only one of four tutors (T1, T2, T5 or T6). Arrows represent the period of time that a tutor occupied one of the four aviaries, and the numbers in the right column indicate the total number of songs tutored by all six tutors. Filled horizontal bars represent the three periods when subjects were exposed to the tutors, and the spaces between the bars represent the two periods when subjects were in social and acoustic isolation, which correspond to times of very low song rates by the song tutors (based on Nordby et al., 2000).

treat juvenile and adult intruders during different developmental periods—summer (the classical sensitive period), autumn and spring (when most late learning seems to occur)—using taxidermic mounts and song playback. Territorial adults responded aggressively to adult intruders throughout the year but were tolerant of juvenile intruders in the summer. In the autumn, territorial adults displayed somewhat reduced aggression towards juveniles, but by the spring they treated them as aggressively as adult intruders. In addition, in the summer trials, we noted that wild juveniles approaching our simulated ‘interactions’ between subjects and adult mounts; these wild juveniles were also tolerated, even at close distances. That juveniles can and do closely approach adults during the early sensitive phase of song learning suggests that direct interactions with adults are possible and might be important for song learning, although notably our observations occurred in the context of the young birds eavesdropping on singing interactions, albeit closely. In contrast, since young birds are treated aggressively in early spring, most late song learning likely happens through eavesdropping or long-distance singing interactions. It seems less likely that late song learning would occur in close interactions, because in face-to-face interactions, song sparrows tend to sing soft song, most often warble song, which is quite different from normal loud song (Akçay, Anderson, Nowicki, Beecher, & Searcy, 2015; Akçay, Tom, Holmes, Campbell, & Beecher, 2011; Searcy, Akçay, Nowicki, & Beecher, 2014).

Field Studies: Shared Songs Are a Valuable Resource

In a series of field experiments, we have shown that, in our population, a song sparrow preferentially uses the songs he shares with a particular neighbour when interacting with him (Akçay, Tom, Campbell, & Beecher, 2013; Beecher & Campbell, 2005; Beecher, Campbell, Burt, Hill, & Nordby, 2000; Beecher, Stoddard, Campbell, & Horning, 1996; Burt & Beecher, 2008; Burt, Bard, Campbell, & Beecher, 2002; Burt, Campbell, & Beecher, 2001). Briefly, a bird initiates countersinging with a neighbour with one of the songs they share, and the neighbour’s reply depends on the context: to escalate the interaction, the neighbour replies with the same song type (‘type matching’); to send a directed but less

aggressive signal, the neighbour replies with a different song that the two birds share (‘repertoire matching’); and to terminate the interaction, the neighbour replies with a nonshared song. Each type of reply thus has a distinct signalling function in a graded signalling system. These different signals do indeed predict subsequent agonistic behaviour, including likelihood of attack, and can fairly be characterized as an honest signalling system (Akçay et al., 2013; Searcy, Anderson, & Nowicki, 2006). For a territorial species such as the song sparrow, the benefit of such a graded signalling system is that it can substitute for more costly forms of negotiating territory boundaries, such as fighting. Indeed, Wilson and Vehrencamp (2001) have found that song sparrows are less aggressive towards neighbours sharing more songs. And as noted earlier, song sharing with neighbours in the bird’s first year predicts the number of years he will survive on territory (Fig. 5; Beecher, Campbell, & Nordby, 2000), suggesting that this pattern of song learning is beneficial to the young bird.

Finally, although we have neglected the possible role of song sharing in intersexual selection, we do have some evidence that females prefer locally shared songs (O’Loughlin & Beecher, 1999). On the other hand, the degree of song sharing with neighbours, as well as song repertoire size, fail to predict extrapair mate choice in our population (on average, 25% of the young in a male’s nest are fathered by neighbours; Hill, Akçay, Campbell, & Beecher, 2011).

Young Birds Do Not Learn More from More Aggressive or Higher-quality Adults

In a field study we tested the role of a specific social factor, the aggressiveness of potential song tutors (Akçay, Reed, et al., 2014). The hypothesis that young birds learn more from more aggressive tutors was proposed over three decades ago, but had been tested only in laboratory studies, and with mixed results (Casey & Baker, 1993; Clayton, 1987; Payne, 1981). 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 found no

effect of tutor aggressiveness, level of aggressive signalling or level of normal singing on an adult bird's tutoring success.

In our earlier study of song learning (Nordby et al., 1999), we looked for correlations between the song-tutoring success and characteristics of the tutors. We examined four quality traits of surviving tutors that might correlate with their degree of influence: (1) song repertoire size, (2) age in the tutoring year, (3) vigour as assessed by the number of years that the tutor survived past the young birds' natal year (1992), and (4) the total number of years that the tutor ultimately survived. We considered only tutors surviving into 1993 to avoid confounding with the late influence effect (e.g. a tutor that died in November or December 1992 might have low influence not because he was a low-quality bird but because he was not present during crystallization of the young bird's repertoire in early spring 1993). We analysed the total tutor scores (i.e. summed across subjects) of the 65 adult males identified as tutors who survived into 1993. Tutor scores were not predicted by any of the proxy variables of tutor quality. We also compared adults identified as tutors ($N = 65$) with those who were not identified as tutors ($N = 22$), again using only those males who survived past 1 January. There were no significant differences between these two groups on any of the four traits we measured.

In summary, these two studies suggest that young song sparrows do not choose their tutors on the basis of the tutor characteristics that one might expect. At the very least, they do not appear to be choosing higher-quality, more aggressive or higher-signalling birds.

DISCUSSION

A Song-learning Strategy?

In summary, our field and laboratory studies taken together suggest that in his first year, a male song sparrow pursues a song-learning strategy correlated with his strategy of establishing and maintaining a territory. The young bird disperses from his natal area at about 30 days of age and moves to an area occupied by adult song sparrows. Adults sing until late July, when they go into moult and are silent for about a month; they resume singing in September, although at a much lower rate. Most young birds hatch in late April, May and June, so all but late hatchers encounter many singing adults for a month or two after hatching, during the classical sensitive period. Some young birds become semiteritorial as early as August, aided and abetted by the adults being in moult, while others wait until autumn or early spring (January and February). For all of these birds, late learning – in the autumn but primarily in January and February – has an important role in shaping their final song repertoire, with birds dropping songs of summer tutors who do not survive into the new year, and keeping songs of their tutor-neighbours who are still present. Social interactions appear to be important in this late learning, but it appears that indirect effects may be as critical as direct effects. In the first summer, adult birds are not aggressive towards juvenile birds, and juveniles seem to be actively attracted to singing interactions they overhear. Intense, face-to-face interactions may not promote song learning, and in fact may be inhibitory, but could play a role in the final stages of song learning as the young bird establishes his territory amongst his tutor-neighbours. Throughout learning, the young bird shows a preference for tutor-shared songs. The result is that if the young bird is able to break in and establish a territory, he will share songs with his tutor-neighbours.

The Tutor's Perspective

If this pattern of song learning is beneficial for the young bird, we may ask whether the bird's tutors benefit as well. Human

language learning has traditionally been viewed as a cooperative enterprise between 'tutor' and 'tutee', e.g. between parent and child, and in some cases birdsong learning may fit this model; for example, zebra finches, *Taeniopygia guttata*, appear to learn from their father (e.g. Goldstein, King, & West, 2003). Some communal breeders and lekking species may present additional examples (Brown & Farabaugh, 1997; Brown, Farabaugh, & Veltman, 1988; Payne & Payne, 1997; Trainer, 1989). But song sparrows follow the much more common pathway of learning songs from older, unrelated birds, after the young bird has dispersed from the natal area. In this circumstance, birdsong learning has generally been viewed as an essentially one-sided enterprise in which the young bird presumably benefits from song learning but no assumptions are made concerning the older tutors. Whether or not song tutoring benefits the older bird is rarely considered, but given that the young bird and his tutor are potentially future competitors, it is possible that tutoring might even be costly for the tutor. In this section, I will consider two hypotheses: the *mutual benefit* hypothesis that both tutor and tutee benefit from the song learning/tutoring interaction, and the *competition hypothesis* that the tutee benefits but the tutor does not (and may even suffer a cost).

A mutual benefit hypothesis of song learning/tutoring can be developed from the 'Dear Enemy' relationship (Fisher, 1954). In this relationship, territorial neighbours show less aggression towards each other than they do towards strangers (Getty, 1987; Jaeger, 1981; Temeles, 1994; Ydenberg, Giraldeau, & Falls, 1988), form defensive coalitions against strangers that threaten territorial integrity (Backwell & Jennions, 2004; Detto, Jennions, & Backwell, 2010; Elfström, 1997), or engage in cooperative defence against predators (Krams, Krama, Igaune, & Mänd, 2008; Olendorf, Getty, & Scribner, 2004). We have shown that song sparrows display the Dear Enemy effect, responding less aggressively to established neighbours than to strangers, but differentiating among their neighbours as well, responding more aggressively to neighbours who have recently been simulated to intrude onto their own territory or onto their neighbour's territory (Akçay, Reed, Campbell, & Beecher, 2010; Akçay et al., 2009; Stoddard, Beecher, Horning, & Campbell, 1991). In addition, they typically respond to the songs of new neighbours with the higher-threat type matching, but to the songs of long-term neighbours with the lower-threat repertoire matching (Beecher, Campbell, Burt, et al., 2000). In eastern song sparrows, Hyman and Hughes (2006) have found that territorial males respond more strongly to aggressive neighbours than to nonaggressive neighbours. In fact, the strength of a male's response to an aggressive neighbour was comparable to his response to a complete stranger (i.e. aggressive neighbours were not Dear Enemies). These individual differences in aggressiveness between song sparrow males have been shown to be stable over time and contexts in both eastern and western populations (Akçay, Campbell, & Beecher, 2014; Hyman, Hughes, Searcy, & Nowicki, 2004).

The Dear Enemy context might form the basis for a mutually beneficial song learning/tutoring strategy. It could be one component of a partially cooperative enterprise between an older bird and a young bird who will become territorial neighbours. The Dear Enemy relationship might begin early on, perhaps even in the natal summer when adults seem quite tolerant of juveniles. As noted earlier there is some evidence in favour of this hypothesis, including the greater survival of young birds sharing more songs with their first-year neighbours, and the finding of Wilson and Vehrencamp (2001) that song sparrows are less aggressive towards neighbours sharing more songs. But these data are equivocal with regard to the mutual benefit hypothesis. First, the song sharing–survival correlation is specific to first-year birds and reflects their first-year sharing only. It may not apply to older birds and, in

any case, sharing changes from year to year as old neighbours die and new birds move in. Second, song sparrows may be less aggressive towards high-sharing birds for other reasons entirely, for example as a direct response to how long they have been neighbours.

The Competition Hypothesis

Although song sparrows show the Dear Enemy effect – they prefer the neighbour they know to the new neighbour they don't know – the birds are still territorial, and the neighbour relationship is still competitive. In addition to fights over territory boundaries, they also engage in extrapair mating at the expense of their neighbours: on average, 25% of the young in a male's nest are the result of extrapair mating, and the extrapair males are always neighbours (Hill et al., 2011). Moreover, males guard their mates against extrapair copulations with neighbours during the female's fertile phase (Akçay et al., 2012). Thus it is certainly plausible that an older bird would not welcome a young bird into or around his territory, and that he might indeed not benefit in the long run by having a new competitor to deal with.

Tutor–Tutee Relationship: Cooperative or Competitive?

One way of differentiating between the mutual benefit (cooperative) and tutee-only benefit (competitive) hypotheses is to look at the effect of tutoring on the survival of the tutor; this method is comparable to our evaluation of the benefits of sharing for young birds (Beecher, Campbell, & Nordby, 2000). If a bird benefits from tutoring via (at least partially) cooperative alliances with his tutees, then birds that tutor more should be more likely to survive on territory than birds that tutor less. Conversely, if tutoring is costly, then birds that tutor more should be less likely to survive on territory than birds that tutor less. Fig. 7 presents a preliminary analysis of survival data for all tutors of the 2009 cohort (Akçay, Reed, et al., 2014). The tutor scores represent the total songs tutored by a bird, and the 89 identified tutors of that year are classified into three groups: those who did not survive past 1 January 2010 ('2009'), those who survived into the 2010 breeding season but not past 1 January 2011 ('2010'), and those who survived until the 2011 breeding season or later ('≥2011', some of whom are still alive). As expected, the 2009-only tutors, being deprived of late influence in the first spring, tutored the least. However, the 2010 tutors tutored more than the tutors who lived into 2011 and beyond. This latter difference was not significant, but it is clearly opposite to the 'mutual benefit' prediction and is in the direction predicted by the 'competition' hypothesis. Further analyses on this and the 2010 and 2011 cohorts (Akçay et al., n.d.) are in progress to see if this trend is genuine. Needless to say, even if it is, this is a correlational study, and other interpretations of such a correlation would be possible. Nevertheless, the data do suggest that older birds do not benefit from tutoring, and may even suffer as a consequence. If this is true, it implies that the tutor and tutee are at least sometimes in significant conflict, and that in the process of working out the conflict the young bird learns the songs of his main competitor. The tutee may often lose this conflict, but we generally will miss these cases because losing tutees die before we can record their crystallized repertoires.

In a recent attempt to characterize the relationship of a bird to his primary tutor (the tutor from whom he learned the most songs), we carried out a playback experiment in which we contrasted a bird's response to his former primary tutor (who had disappeared in the recent past) with the bird's response to a stranger. By way of background, we have never found a bird to respond more strongly to a present or recent neighbour than to a stranger (reviewed in

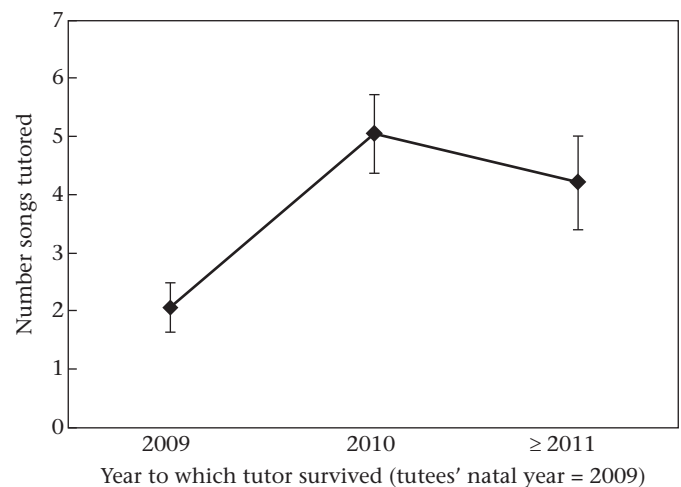


Figure 7. Tutors that died before the tutees' first breeding season (2010) tutored slightly more than tutors that lived to 2011 or longer (means and standard errors shown; the difference between the 2010 and ≥2011 tutors was not significant). Tutors that were alive in the summer of 2009 (the hatch year of this group of tutees) but that did not survive to 1 January 2010 would have been largely deprived of late influence on the tutees' song learning; thus, we expected them to tutor less on average, as they clearly did.

Beecher, 2008). However, in this experiment, birds responded more aggressively to the songs of their primary tutors than they did to songs of strangers, and the degree of this difference was positively correlated with how many songs a bird had learned from his primary tutor (Akçay et al., n.d.). This finding is consistent with the hypothesis that the relationship between tutor and tutee is competitive rather than cooperative.

Is Song Sharing Generally Advantageous and, If So, Why?

One advantage of plasticity is that a bird can copy the songs of group mates or territorial neighbours, and thus share songs with them. Most studies that have examined neighbours for song sharing in repertoire species, or song similarity in single-song species, have found greater similarity between neighbours than between non-neighbours (Avery & Oring, 1977; Beebe, 2002; Briskie, 1999; Demko, Reitsma, & Staicer, 2016; Koetz, Westcott, & Congdon, 2007; McGregor & Krebs, 1982; McGregor & Thompson, 1988; Molles & Vehrencamp, 1999; Nelson, 1992; Payne, 1982, 1985; Schroeder & Wiley, 1983; Verner, 1975). There are other populations, however, where birds share no more with neighbours than with other birds in the population (e.g. chaffinches, *Fringilla coelebs*: Slater & Ince, 1982; western meadowlarks, *Sturnella neglecta*: Horn & Falls, 1988; Kentucky warblers, *Geothlypis formosa*: Tsipoura & Morton, 1988; Gambel's white-crowned sparrows, *Z. l. gambelii*: Nelson, 1999) and of special interest here, most eastern song sparrow populations (Hughes et al., 2007). Some of these exceptions to the rule may reflect the very conservative sharing criteria used by the researchers. Nelson and Marler (1994) have argued that in many populations, especially migratory populations, birds may memorize songs from one set of birds in their natal summer and then, in the following spring, select from this large pool of songs those songs that best match the songs of totally different birds who are now their neighbours. This process would produce populations where neighbour song sharing might not pass the song-sharing threshold applied by one researcher group but might be detectable by someone looking for more subtle similarities. An excellent example has been provided by Nelson (1992). Field sparrow, *Spizella pusilla*, males return to the breeding area

with two or three songs in their repertoires; Nelson showed that they retained the song that most closely resembled the song of the most actively singing neighbour (although the song similarities might not have satisfied the usual song-sharing criteria). In any case, the degree of song similarity between neighbours will surely be greater in populations where birds learn their songs directly from their neighbours than in cases where they follow the more indirect Nelson–Marler selection process.

We have suggested that song sharing with neighbours appears to be the ‘goal’ of the song sparrow’s song-learning strategy. Besides the hypothesis already suggested that having shared songs facilitates communication with the young bird’s new neighbours, several other hypotheses have been developed over the years for why song sharing might be advantageous (see Beecher, 2008).

According to the *genetic adaptation* hypothesis (Baker, 1975; Nottebohm, 1970), males learn songs and females develop their song preferences before dispersal. Thus the male’s song dialect is a reliable indicator of his natal area and the female uses the male’s song as a means to choose a male from the same natal area as herself, thus presumably gaining a mate with the same local (genetic) adaptations. This theory requires (1) an adaptive correlation between geography and population genetic structure, (2) a predictive correlation between dialect and population genetic structure, (3) males learning songs before natal dispersal, and (4) females choosing mates that sing the local dialect. There is little direct support for the genetic adaptation hypothesis; in particular, assumption 3 is rarely true.

The *mimicry* hypothesis of Craig and Jenkins (1982) focuses on the male–male competition context. According to this hypothesis, immigrant or first-year birds entering the population mimic the songs of the established territory-holding birds to gain an advantage in establishing their own territories. The advantage presumably arises from the newcomer’s being confused with established birds and thereby receiving reduced aggression. The mimicry hypothesis has received little support, and in particular is inconsistent with the many experiments showing well-developed individual recognition in songbird species with song sharing and repertoires (reviewed in Stoddard, 1996). In a playback experiment that tested this hypothesis about as directly as can be done, Wilson and Vehrencamp (2001) compared the aggressive response of song sparrows to (1) neighbour songs, (2) stranger songs that were highly similar to (i.e. ‘mimicked’) neighbour songs and (3) non-mimic stranger songs. The birds responded just as aggressively to mimic stranger songs as to nonmimic stranger songs, and more aggressively to either than to neighbour songs.

The *badge* hypothesis has been formulated most explicitly by Rothstein and Fleischer (1987) and by Lachlan, Janik, and Slater (2004), and more informally in several other papers (Beecher et al., 1997; Brown & Farabaugh, 1997; Wilson & Vehrencamp, 2001). According to this hypothesis, shared songs serve as a badge of familiarity in groups and among territorial neighbours. Indeed, Beletsky and Orians (1989) have shown that male red-winged blackbirds, *Agelaius phoeniceus*, with familiar neighbours have greater breeding success than do males with unfamiliar neighbours. Neither preferring nor cooperating with familiar neighbours requires shared songs, of course, but shared songs are a reliable signal of familiarity or locality since they must be learned in the local neighbourhood.

The companion version of the badge hypothesis is that females prefer local males because of various advantages they have over immigrant males, and learned area songs are a reliable signal of a background in the local area. This hypothesis is similar to the genetic adaptation hypothesis, but more general as to the proposed mechanism of the local advantage. Familiarity with the local area is generally thought to provide numerous advantages to an individual

(Davis & Stamps, 2004). Thus, it might benefit a female to choose a male singing local song (a reliable signal that it has been in the area for some time) over a male singing nonlocal song (reliably signalling that it has arrived only recently). The badge hypothesis is also different from the genetic adaptation hypothesis in assuming that song is learned *after* dispersal from the natal area rather than before (although if dispersal is not far, this distinction could be irrelevant).

The *communication* hypothesis developed in this paper – the idea that song sharing benefits the young bird by facilitating his ability to communicate with his neighbours – is not inconsistent for the most part with the preceding hypotheses, but it does fit especially well with the badge hypothesis. For most territorial songbirds, song is a long distance signal intended for adjacent or once-removed territorial neighbours, with much of this communication happening with the birds out of sight of one another. Songbirds have no fences, and territorial boundaries must be constantly reaffirmed, and on occasion, renegotiated. For example, a male’s mate may decide that the perfect spot for her nest is just over what has been the boundary. Or a neighbour may have been recently predated, leaving some prime territory up for grabs between several of his neighbours. Song is critical to boundary negotiations, for it provides a nonviolent way of ‘negotiating’ these disputes. For the most part, this communication appears to be honest (e.g. Akçay et al., 2013). In the case of our western song sparrows, shared songs are at the heart of song communication between neighbours.

The hypotheses discussed in this section are not mutually exclusive, and it is possible that some combination of these hypotheses (and perhaps others not discussed here), will ultimately be seen to account for the commonly observed song sharing in songbird populations, and hopefully for the apparent exceptions to this rule.

Eastern versus Western Song Sparrows

If a song-learning programme should equip a bird with songs that he shares with birds that will be his long-term neighbours, then what is the best song-learning strategy in populations where neighbours change between breeding seasons, or perhaps within the breeding season as well? Kroodsma (1996) has argued that for birds that will not have long-term neighbours, there is no advantage to shared songs, and so the development of generalized species-typical songs will be favoured. The sedge wren, *Cistothorus platensis*, provides an illustration of this prediction. Northern populations of sedge wrens are migratory, and during the breeding season, they are seminomadic as well. Thus, even in the breeding season, they have a constantly changing set of neighbours. These sedge wrens show a unique pattern of song learning in tape tutor experiments: they do not imitate tutor songs but rather improvise songs (different but derived from the tutor songs) or invent songs (totally new), all of them normal species songs (Kroodsma, Liu, Goodwin, & Bedell, 1999; Kroodsma & Verner, 1978). Consequently, each bird winds up with a repertoire of unique songs, and two neighbours in the field (who probably will not be neighbours for long) will share no song types. In contrast, the closely related but sedentary marsh wrens, *Cistothorus palustris*, faithfully copy tutor songs in comparable experiments, and in the field share songs with their neighbours (Kroodsma & Pickert, 1984; Verner, 1975). Furthermore, tropical populations of sedge wrens are sedentary, in contrast to the seminomadic northern populations, and these tropical sedge wrens show the common pattern of song sharing with neighbours that is generally taken to imply song learning from neighbours (Kroodsma, Sanchez, et al., 1999).

Although eastern song sparrows are at least partially migratory, their demography does not appear to be that different from

that seen in our western population. Hughes et al. (2007) found that both annual survival of territorial males (about 60%) and territory tenure times are no different from our Washington population. Furthermore, approximately three-quarters of eastern males that return between years have territories in the second year that overlap their territories in the previous year. Thus, there is considerable stability in the territorial system, which should lead to there being long-term neighbours. If there are any differences in the degree of stability between these two populations, these differences appear to be quantitative rather than qualitative. However, despite their similar demography, which would seem to predispose to song sharing, sharing is much weaker in the eastern population (Hughes et al., 2007): 8% sharing between neighbours in the Pennsylvania population versus 24% sharing in the Seattle population (Dubois et al., 2015). Moreover, Pennsylvania birds do not repertoire-match as do birds in western populations. In addition, a migratory eastern population in Ontario has been found showing a high level of sharing (Foote & Barber, 2007), further complicating the problem of explaining sharing levels.

As I concluded in an earlier review of this problem (Beecher, 2008), if the demographic differences between these two populations are as minor as they seem so far, the different ways in which males in the two populations learn and use their songs undermine the interpretation of the song-learning 'strategy' of western song sparrows I have offered in this paper. Thus, the final question here is whether song learning in song sparrows from the two populations is truly different, or whether the quantitative differences in song sharing between the two populations results from different types of song tutoring related to as yet undetected demographic differences. As I suggested earlier (Beecher, 2008), the logical experiment to settle this question would be to raise young birds from both populations in the laboratory under a common tutoring regime (common garden experiment, Kroodsma & Canady, 1985). For example, the song repertoires of western marsh wrens are about twice as large as those of eastern marsh wrens when measured in the field, and this difference persists when young birds from both populations are raised in the laboratory under a common tutoring regime (Kroodsma & Canady, 1985). Marler and Peters' (1988a, 1988b) comparison of song sparrows and swamp sparrows with respect to repertoire size and song selectivity, and Nelson and colleagues' comparison of different white-crowned sparrow races with respect to several aspects of song development (Nelson, 1999; Nelson, Marler, & Palleroni, 1996; Nelson, Whaling, & Marler, 1996; Nelson et al., 1995) also reveal striking differences between the two populations or species when exposed to a common tutoring regime, indicating differences in the genetic–developmental programme underlying song learning. I hope that in the future it will be possible to carry out a common garden experiment that would examine whether the song learning programmes of eastern and western song sparrows are as fundamentally different as studies to date seem to suggest.

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