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Friends and Enemies: How Social Dynamics Shape Communication and Song Learning in Song Sparrows

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INTRODUCTION

Songbirds have been a central focus for animal behaviorists studying the social, ecological, and evolutionary processes that influence behavior. Their song has long fascinated naturalists, and the relative ease of capturing, marking, and observing songbirds has enabled detailed studies of known individuals. Several model songbird species have emerged through decades of research. The song sparrow (*Melospiza melodia*) is one of them. Starting with the pioneering work of Margaret Nice (Nice, 1937, 1943) and continuing through the studies of population dynamics on Mandarte Island in British Columbia (e.g., Smith, 1984; Smith et al., 2005; Smith & Zach, 1979), song sparrows have been a major model system in North America for answering questions about behavior and evolution. Here we describe the results of our own studies on song sparrows, ongoing since 1986 in Discovery Park, Seattle, Washington. We focus on one major facet of our research, the question of how social dynamics in this population have shaped the song system the birds use to communicate and how it may have shaped the process of song learning.

In many ways, song sparrows are the archetypical temperate songbird: they get their name from their beautiful, complex song, and, like most songbirds, they learn these songs. A male song sparrow—only males sing in this species—learns his songs during his first year of life, the process ending when he is 9 to 10 months old and beginning his first breeding season. A major function of song sparrow song is to mediate a male's interactions with his territorial neighbors.

Song sparrows pair up ***monogamously*** and maintain ***territories*** that are large enough for most of their ***foraging*** (though they do forage off the territory some of the time). Both parents contribute roughly equally to ***parental care*** (although the female does all the incubation) and in a good year may fledge two clutches in a breeding season. Although pairs are socially monogamous, they are not genetically monogamous, as about 25 percent of the young in a nest are fathered not by the social mate but by one or more of the neighboring males (O'Connor et al., 2006; Sardell et al., 2010; Hill et al., 2011). ***Extra-pair mating*** appears to be the rule and not the exception in songbirds (Griffith et al., 2002; Westneat & Stewart, 2003), and the 25 percent extra-pair parentage rate seen in song sparrows is about average for a songbird species. The bulk of territory defense is handled by the male, with song being one important tool in the male's defense arsenal. First and foremost, by singing from various posts within his territory, the male indicates the extent and boundaries of his territory while signaling that he is home, ready to defend it against any intruder. In addition to singing to "post" his territory, the male can communicate, at a distance, with his neighbors. In particular, two ***countersinging*** males can use song to negotiate and remind each other of the location of the boundary that separates their territories. These negotiations are generally most intense in early spring before the onset of the breeding season, especially between new neighbors (about 30 to 40 percent of song sparrows in our population do not survive over winter).

DEAR ENEMIES

As is the case in many territorial species, long-term neighbors have an interesting relationship, one that is partially competitive but also partially cooperative. For the territorial male, his neighbor is a competitor for matings (fertilizations), for food on the territory, and for the territory itself. At the same time, however, he prefers the neighbor he knows to a new neighbor he does not know because a new neighbor will not know and therefore not respect the present boundaries and will extract costs in time and effort to reestablish them. Thus the relationship of the territorial neighbors has been dubbed a "dear enemy" relationship (Fisher, 1954; Temeles, 1994). We focus on this relationship in this chapter and attempt to show how it affects both the song communication system and the song-learning program of song sparrows.

The dear enemy relationship is a reciprocal relationship. Just as a bird will prefer the neighbor he knows to one he does not, so will his neighbor have the same preference. Thus both of them should have a mutual interest in keeping out interlopers and should cooperate to keep them out. However, such reciprocity is difficult to demonstrate—because the interests of each individual are essentially identical, cooperation is not easily distinguished from pure self-interest. Nevertheless, in this chapter we will show that song sparrows do meet several of the conditions required for a dear enemy relationship. We will then show how their song communication system helps them maintain this relationship, and, finally, how it may affect the nature of song learning in this species.

Students of behavior naturally hope to generalize at least some of their findings from their study species to other species. In our case we want to generalize our findings at least to other songbirds that have similar social systems. However, it turns out that it is a challenge to generalize even to other song sparrow populations, as this widely distributed species (covering virtually all of North America) is quite diverse geographically. Presently 24 subspecies of song sparrows have been identified (Patten, 2001; Arcese et al., 2002). Moreover, there is already considerable evidence of differences between western (*M. melodia melospiza*) and eastern (*M. melodia melodia*) populations. It is not clear whether these differences are ***proximate*** effects or ***ultimate*** effects of environmental and life history differences. In this chapter, we will comment from time to time on these east-west differences but will talk mostly about our western study population.

Background: Song in Song Sparrows

Song sparrows are like most songbirds in having multiple ***song types*** ("***song repertoires***"). Rarely will a song sparrow have fewer than 6 or more than 12 song types, and most birds have repertoires ranging from 7 to 11 types. When a song sparrow is "free singing" (i.e., simply posting his territory, or when unpaired, singing to attract a mate), the bird uses his song types interchangeably, singing one type for a while before switching to another for a while; that is, singing with ***eventual variety*** (in contrast to ***immediate variety*** singing, where the bird changes song types after every song). When a song sparrow switches song types, he generally turns to the song type he has not sung for the longest while. Nevertheless, although he avoids recently sung types, he does not sing his types in a particular order, so the order you observe on one day will be randomly different from the order you observe on another day.

Like most songbirds, song sparrows learn their songs. This learning occurs in their first year; a bird does not modify his song repertoire after the first year.

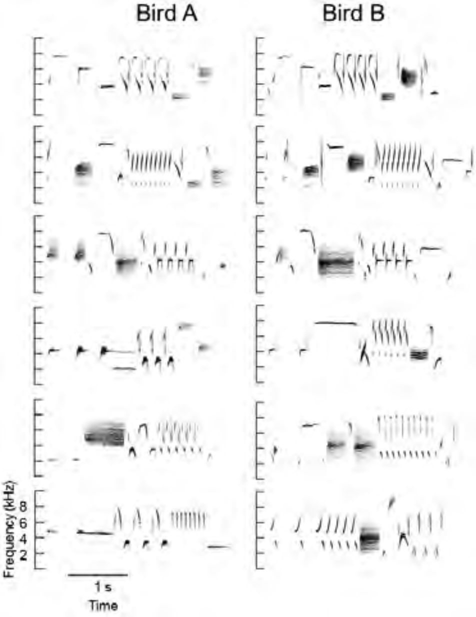

Figure 2.1. Partial song repertoires of two song sparrows. Birds A and B were neighbors and shared the first three songs in their nine-song repertoires (33% sharing). The shared songs of birds A and B are shown in the top three rows, while six of their remaining unshared types are shown in the bottom three rows. Frequency (vertical) scale: 0-10 kHz, markers at 2-kHz intervals. Songs are 2 to 3 seconds long.

Because, in our western population, a song sparrow begins song learning after he disperses from his natal area and typically learns his songs in the neighborhood in which he will ultimately settle, his final repertoire consists of "local" songs, and he will usually share song types with his neighbors. Thus a bird might settle next to an older bird from whom he learned some of his songs, or next to a bird with whom he has some "song tutors" in common; other more complicated "lines of descent" in song learning are possible of course. A typical result is shown in Figure 2.1, in which two neighboring song sparrows share four of their nine songs.

Background: The Playback Experiment

The major method used in the studies discussed in this chapter—and indeed in most studies of song communication in birds—is the ***playback experiment***: recordings of an animal vocalizations are played back to the subject, and its response is observed. Playback can consist of the animal's own vocal signals, but most often they are another animal's signals. Playback experiments are essentially simulations: the experimenters attempt to simulate a natural occurrence, but one in which they can control the location, timing, context, delivery, and acoustical characteristics of the playback. The first playback experiments were carried out with songbirds, with the goal of determining if birds could distinguish between local and nonlocal dialects, or between neighbor and stranger songs (Weeden & Falls, 1959). In the experiments we describe in this chapter, we most often have tried to simulate a particular neighbor, usually singing from his own territory but sometimes singing from within the subject's territory (a simulated intrusion). We have also simulated strangers, either on or off the territory, and juvenile birds singing song that is not fully developed. For playbacks from outside the territory, the simulation is realistic because song is a long-distance signal most often sung by a bird that is out of sight or obscured by foliage. However, for intrusions onto the territory or on occasions when the subject gets close to the playback, the simulation is less realistic because real birds do not both hide and sing full-throated song at the same time. In some cases we have enhanced the simulation by using a taxidermic mount (a stuffed bird) of a song sparrow. Subjects in this case will direct their attention to the mount, often giving aggressive displays—wing waves (see Figure 2.2) and soft song (discussed further below) and often attacking it. Although the mount does not move—clearly a robot would be ideal—it does provide the subject with a plausible source of the song he is hearing as well as an actual "intruder" to attack. We have discovered that we can make this simulation most realistic by placing the mount in the foliage of a bush or a tree in a natural singing position and by using a small (and thus

Figure 2.2. A male song sparrow wing-waving, an aggressive signal. Note color bands on legs by which the bird is individually identified. (Photo by Çağlar Akçay)

relatively inconspicuous) loudspeaker placed close to the mount. When the mount is so placed, over half of subjects will attack it within 15 minutes (Akçay et al., 2013).

Song Sparrow Neighbors Are Dear Enemies

In our western population, song sparrows establish their territories sometime between the autumn of their natal year and the following spring. They will usually stay on this territory for the rest of their lives, with only minor shifts of territory boundaries or perhaps a lateral move into the vacated territory of a deceased neighbor. The average territory tenure for a bird is two to three years, although individuals can last for as long as seven or eight years. Consequently birds typically have long-term neighbors. Moreover, they typically have dear enemy relationships with these long-term neighbors. We describe here three experiments that illustrate this situation.

One prediction of the dear enemy hypothesis is that a neighbor singing near the territory boundary but still within his own territory should be tolerated. However, a stranger singing from that very same spot, or a neighbor singing from a different ("wrong") boundary, should not be tolerated. This is because a neighbor singing from a wrong territory would be a prospecting bird and a potential threat, just as a new, arriving stranger singing from anywhere would be. Philip Stoddard and colleagues (Stoddard et al., 1991) carried out a playback experiment to test how a song sparrow would respond to neighbor versus stranger song played from three locations: from within the neighbor's territory near the boundary, from the opposite territory boundary, and from within the subject's territory (simulating an intrusion). As predicted, these researchers found that song sparrows responded weakly to a (simulated) neighbor singing near their mutual boundary but strongly to a stranger singing from this same location. In contrast, subjects responded strongly to both neighbor and stranger singing from the opposite boundary (where that neighbor does not normally sing). And they responded yet more aggressively to song from the center of their territory, equally aggressively whether it was stranger song or neighbor song (Figure 2.3).

A second prediction of the dear enemy hypothesis is that the tolerance shown to neighbors normally should dissipate if the neighbor violates their agreed mutual boundary. We simulated such a boundary violation with a two-stage playback experiment (Akçay et al., 2009). The design is illustrated in Figure 2.4(a). In the first stage, we simulated a neighbor intruding into the subject's territory. The simulated intruding neighbor sang from the center of the subject's territory for 2 minutes. The second stage began after a wait of 45 minutes and consisted of two successive playbacks, each one simulating a

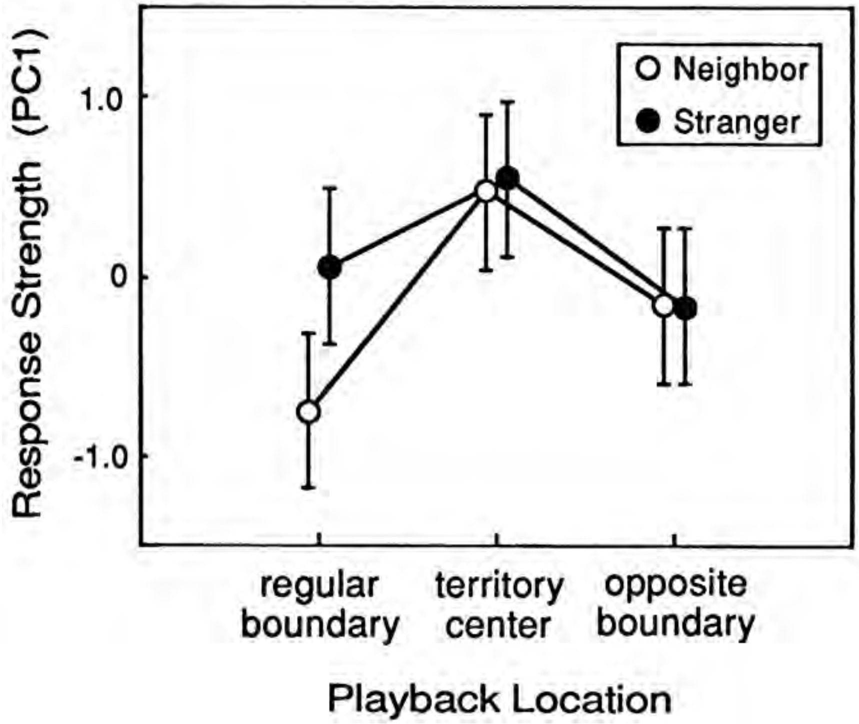

Figure 2.3. Response during playback of 14 male song sparrows to songs of neighbors and strangers played in three locations: the regular boundary of the neighbor that sings the N song (where the neighbor song is normally heard), at the center of the subject's territory, and at the boundary opposite the boundary of the subject and his neighbor. Response scores refer to the first component (PC1) of a principal component analysis on number of flights and closest approach to the playback speaker. Error bars are ≥2 SE. (From Stoddard et al., 1991. Reprinted by permission of Springer Publishing.)

neighbor singing from his boundary with the subject. In one playback we played songs of the earlier (simulated) intruder, this time from the intruder's own territory, just on his side of the boundary. In the other playback, we played the songs of a neutral neighbor from just on his side of their mutual boundary. These boundary playbacks were separated by 15 minutes, and their order was ***counterbalanced*** across subjects. We predicted that if males keep track of the behavior of their neighbors and retaliate specifically against those who have violated the boundary agreement, that they should respond more strongly to the boundary playback of the neighbor who had earlier intruded

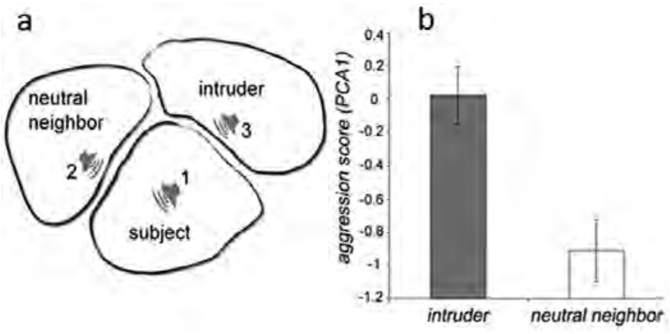

Figure 2.4. (a) Experimental design of Akçay et al. (2009). Each trial started with an intrusion on the subject's territory (1), followed by two boundary playbacks from the intruder's boundary and the neutral neighbor's boundary (2 and 3; the order of these were counterbalanced across subjects). (b) Results from Akçay et al. (2009). Aggression scores refer to the first component (PC1) of a principal component analysis on three variables: rate of flights, closest approach, and latency to respond. Higher scores indicate higher aggression. Error bars are ≥1 SE. (Based on data from Akçay et al., 2009)

than to the boundary playback of the neutral neighbor. Indeed, our results showed that subjects responded significantly more aggressively towards neighbors who recently intruded upon their territory (Figure 2.4[b]).

A further prediction of the dear enemy hypothesis is that a bird should base his assessment of his neighbor not only on his direct experience with that neighbor but on his observation of that neighbor's interactions with other neighbors. Birds with multiple neighbors have ample opportunity to ***eavesdrop*** on the interactions of these neighbors with one another and identify the breaking of a truce between two neighbors through eavesdropping. If a neighbor breaks the truce with another neighbor, then he is more likely to be an aggressor to oneself as well. We therefore carried out another playback experiment and predicted that a song sparrow would (1) eavesdrop on a simulated intrusion of neighbor A on neighbor B and (2) use this information in calibrating his aggressiveness toward these neighbors in subsequent interactions. Specifically, we predicted that subsequently he would behave more aggressively toward the intruding neighbor singing from his boundary than toward the victimized neighbor singing from his (Akçay et al., 2010).

Some recent theoretical work has challenged this prediction. In a model of eavesdropping in agonistic interactions, Johnstone and Bshary (2004) found that the presence of eavesdroppers increased rather than decreased their overall aggression. The logic is that it pays to be more aggressive in the presence of eavesdroppers to discourage the eavesdroppers from challenging the aggressive individual later on. Thus this model actually predicts that eavesdropping neighbors should decrease their aggression towards aggressive neighbors.

To test whether neighbors increase or decrease aggression (retaliate or do not) against aggressive neighbors, we carried out a playback experiment that used a design similar to that of the previous experiment (Figure 2.5a). The main difference was that the simulated intrusion was not on the subject's territory but on another neighbor's territory (we term this neighbor the victim). We fitted the subjects with radio transmitters before the experiment to be able to monitor their behavior during the intrusion on their neighbor. We predicted subjects would show some interest in the intrusion happening next door and approach the boundary of the victim.

After the intrusion, we tested the subject's responses to the intruder and the victim from their respective boundaries with the subject in the same way as in Experiment 1 (the victim and the intruder were again randomly chosen from among the subject's neighbors, and the order of boundary trials were counterbalanced). If subjects have eavesdropped on the simulated intrusion by their neighbor, the intruder, onto the territory of the other neighbor, the victim, and further were able to assign correctly the roles of "defecting" versus simply

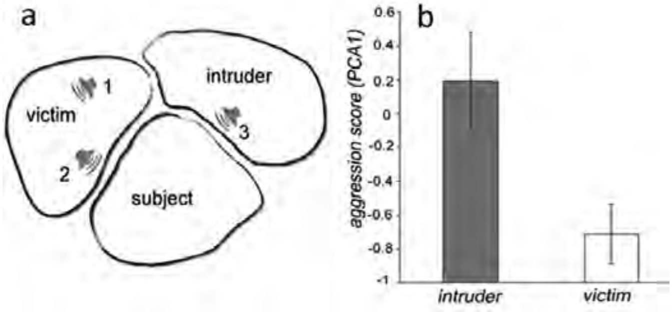

Figure 2.5. (a) Experimental design of Akçay et al. (2010). Each trial started with an intrusion (1) on the victim's territory, which was adjacent to the subject's territory. The boundary playbacks from the victim and the intruder (2 and 3, order counterbalanced across subjects) were directed to the subject, who did not receive the intrusion himself but had eavesdropped on it. (b) Results from Akçay et al. (2010). Aggression scores refer to the first component (PC1) of a principal component analysis on three variables: rate of flights, closest approach, and latency to respond. Higher scores indicate higher aggression. Error bars are ≥1 SE. (Based on data from Akçay et al., 2010)

defending one's own territory, they should retaliate against (respond more strongly to) the intruding neighbor.

Our results showed that subjects did in fact increase aggression towards neighbors who had recently intruded on another neighbor's territory (Figure 2.5b). Furthermore, 8 out of 10 subjects approached the subject's boundary during the intrusion, indicating that they were indeed interested in the intrusion. This is the first evidence for eavesdropping in a territorial system with repeated interactions between familiar individuals. In other words, an aggressive individual will acquire a bad reputation in the eye of eavesdropping neighbors and is likely to face retaliation from these neighbors. We identify this threat of retaliation by eavesdropping neighbors as an additional factor promoting dear enemy cooperation between neighbors, contrary to the suggestions of models of eavesdropping in agonistic contexts (Johnstone, 2001; Johnstone & Bshary, 2004).

HOW DO SONG SPARROWS COMMUNICATE?

The above studies demonstrate that song sparrows recognize their neighbors and keep tabs on them through their direct experience with them as well as by eavesdropping on interactions between neighbors. Now we turn to the question of how song sparrows communicate with their neighbors through their songs.

For song sparrows, song is a long-distance signal intended for adjacent or once-removed territorial neighbors. Typically the birds that have a singing interaction are out of sight of one another. This is the prototypical case for songbirds and explains why such small birds produce such loud sounds. Most of the rest of their vocal repertoire is much softer. At the heart of the song repertoire is the posting function—the bird is both notifying his neighbor that he is still there occupying his territory and marking the extent of his territory. Songbirds have no fences, and territorial boundaries need to be constantly reaffirmed. Indeed, they may need to be 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 neighbor may have been picked off by a hawk, leaving some prime territory up for grabs between several of his neighbors. Song is critical to boundary negotiations, for it provides a nonviolent way of "negotiating" these disputes.

In our population of song sparrows, birds appear to follow a set of conventions predicated on how they use the songs they happen to share (Figure 2.6). As an example, consider the two neighbors whose repertoires are shown in Figure 2.1. Suppose Bird 1 decides that their mutual boundary should be a

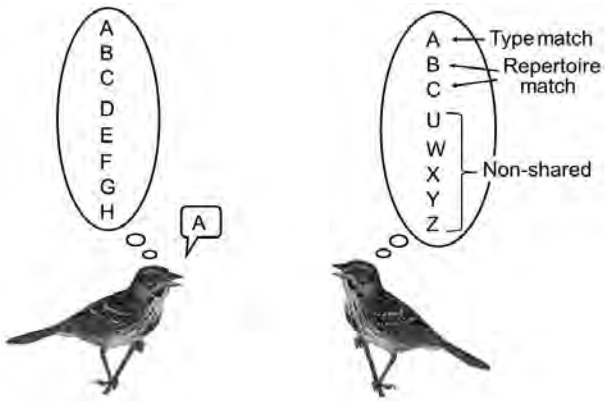

Figure 2.6. Cartoon illustrating how song sparrow neighbors communicate using shared songs. A bird typically addresses a neighbor by singing one of the songs they share. The neighbor can reply by singing the same song type (type matching), singing a different song type that he shares with that neighbor (repertoire matching), singing a song type he does not share with that neighbor, or not singing at all. Type matching appears to be an escalation and singing an unshared song a deescalation, while repertoire matching is an intermediate but directed signal.

few meters into Bird 2's territory, and he aims to establish this new boundary. They share four of these songs—we will call them types A, B, C, and D—but no others. Bird 1 can "address" bird 2 by singing one of their shared types A, B, C, or D (in the direction of bird 2 because other neighbors may also share some of these types). Let us say bird 1 sings A. Bird 2 then can "acknowledge" the signal by replying with B, C, or D (***repertoire matches***), reply with A (***type match***), sing one of the unshared types, or ignore by not singing at all. If bird 2 type matches bird 1 (sings A), bird 2 can then continue to sing that song type ("stay on type"), can switch to another shared song (repertoire matching; Beecher et al., 1996), switch to an unshared type, or disengage totally by stopping singing. Note that to type match, the bird need have no prior experience with his opponent—the bird simply replies with his most similar song, and generally the match' will be perceptually obvious. But to reply with a shared song or with an unshared song, the bird needs to have had some experience with his neighbor—the bird needs to know which songs the two share and which they do not. This pattern of singing does not normally develop until birds have been neighbors for some period of time.

These "singing conventions" are summarized in Figure 2.7. It turns out that each convention—type matching, repertoire matching, and switching

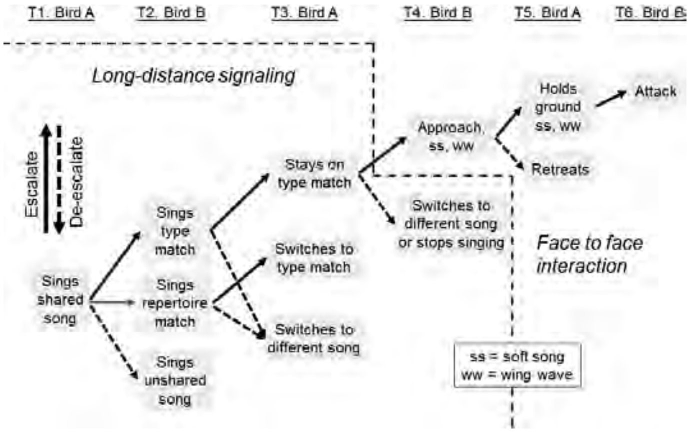

Figure 2.7. Schematic diagram of an interaction between two neighboring song sparrows. Birds A and B interact during six time periods (T1-T6), each of which contains a change of state. Aggressive escalations are indicated with upward (solid line) arrows, and deescalations with downward (dotted line) arrows. For simplicity the diagram focuses on escalations. The interaction begins when the two birds are at a distance, on their own territories, and probably out of visual contact, but as the interaction escalates, the birds approach one another and are presumed to be within a few meters of one another to the right of the dotted line. The signal and response alternatives of each bird are indicated vertically, with more aggressive alternatives above less aggressive ones. The song sparrow signaling system depends on the fact that two territorial neighbors will share some of their 7 to 10 song types and not others. At T1, bird A engages his neighbor by singing a shared song. At T2, the neighbor (bird B) can escalate by replying to that shared song with a type match (the same song type), deescalate by singing an unshared song, or reply at an intermediate level with a repertoire match (a different song type they share). If bird B repertoire matches (the most common reply for established neighbors), then at T3, bird A can escalate by type matching or deescalate by singing a different song type (either an unshared song type or a different shared type—i.e., another repertoire match). If bird B instead type matches at T2, then at T3, bird A can either maintain escalation by staying with the type match or deescalate by switching song types. At T4, the birds should be close, and bird B can escalate by switching to soft song. Bird A can meet the escalation by switching to soft song, or he can retreat (T5). Soft song is the strongest aggressive signal in the hierarchy, and at this point (T6), soft song is most likely followed by attack. In this system, the type matching is a poor predictor of attack because several layers of contingency intervene between B's initial decision on whether to type match and his final decision on whether to attack. Type matching can still be viewed as an aggressive signal, however, because it does predict escalation in the interaction. (This model is based primarily on Beecher et al., 1996; Beecher, Campbell, Burt, et al., 2000; Burt et al., 2001; Beecher & Campbell, 2005; and Akçay et al., in press.)

off—has a distinct signaling function in a ***graded*** signaling system, with type matching signaling a willingness to escalate, repertoire matching a willingness to continue the interaction but not necessarily escalating, and switching off signaling deescalation. We now turn to the evidence decoding this code.

The Song Sparrow Code

In the first study contrasting the different functions of singing conventions, we used a prediction that follows from the dear enemy relationship between neighbors. As mentioned above, early in the spring most neighbors are in the process of negotiating their boundaries, inevitably involving more aggressive interactions. Later in the spring, however, most boundaries have been established and are stable, and neighbors are in the dear enemy relationship of watchful tolerance of each other. If type matching is a signal of willingness to escalate and repertoire matching a willingness to acknowledge the opponent but not necessary escalate, we predicted that type matching in response to a neighbor should be much more common early in the spring and repertoire matching much more common later in the spring. In line with the hypothesis, early in the spring (mid-April) most subjects (8 out of 11, 73%) replied to a neighbor's shared song played from that neighbor's boundary with a type match, the rest replying with a repertoire match. In contrast, late in the spring (late May to early June), only 18 percent of subjects responded to their neighbor's shared song with a type match, the rest replying with a repertoire match (Beecher, Campbell, Burt, et al., 2000), again in line with the hypothesis that type matching is an escalation signal whereas repertoire matching is not.

Further evidence for the signaling system in Figure 2.7 came from an interactive playback experiment that our group carried out in 1997 and 1998 (Burt et al., 2001). In this experiment, we wanted to more directly test the hypothesis that type matching is a signal of willingness to escalate (i.e., a threat signal) by assessing how birds responded when they were type matched versus repertoire matched. To that end, we set up the playback equipment at the boundary of the subject whose singing we were going to simulate and waited until the subject sang a song that was shared with this particular neighbor (not a task for the impatient!). Then, when the subject sang a shared song (we were able to view the sonograms of the songs that the subject sang in real time on a laptop), we "replied" with the neighbor's version of the song (type match), another shared song (repertoire match), or a stranger song (song recorded from a bird at least a kilometer away) and noted several measures of approach and aggression. The prediction was that when subjects were type matched by their simulated neighbor, they would respond as if they had just been threatened, specifically, more aggressively than if the simulated neighbor had repertoire matched them. The stranger-playback condition was meant to provide a reference for comparison of the level of aggression to the neighbor (subjects should respond most strongly to the stranger).

The results were clear—as expected, subjects were most aggressive when they were countered with a stranger playback. Crucially, subjects were significantly more aggressive in response to being type matched compared to being repertoire matched by the simulated neighbor (Burt et al., 2001). Furthermore, among the trials where the subjects were type matched, the most aggressive birds were those who stayed on the same type upon being type matched. This suggests that not only is type matching a signal of escalation, so is staying on the same type when you are being type matched by the opponent. Thus, these two experiments established that type matching and repertoire matching signal different levels of threat from the signaler. In a more recent study (Beecher & Campbell, 2005), we tested the function of singing an unshared song using a design similar to the above study and found that following a simulated intrusion and retreat by a neighbor, subjects reduced their aggressive response and departed the scene sooner if the retreating neighbor sang an unshared song than if he sang a shared song. We also found that birds responded more quickly when a neighbor singing from their territory boundary sang a song the two shared than when he sang a song they did not share. All in all, these studies make a strong case that song sparrow males perceive type-matching songs, repertoire-matching songs, and unshared songs as part of a graded signaling system with type matches being the highest threat, unshared songs the least threatening, and repertoire matches intermediate in threat.

The Code Reconsidered

We thought we had cracked the song sparrow code when a new study cast doubt on the idea that type matching was a reliable threat signal. In this study of an eastern U.S. song sparrow population (Pennsylvania), Searcy and colleagues (Searcy et al., 2006) challenged song sparrows with a simulated intrusion by playing the bird his own song (“self-song”) from the middle of his territory. They measured a host of responses, including several putative aggressive signals such as wing waves and soft songs, as well as whether or not the bird type matched the playback (using self-song removes any doubt about whether the subject’s reply song is the same type or not). Then, after five minutes of playback, they revealed a taxidermic mount of a song sparrow that was attached to the speaker, giving the angry subject a target to attack. The aim was to assess how reliable each signaling behavior was in predicting a subsequent attack that seemed likely to await the hapless mount. To their surprise, only about 20 percent of subjects actually attacked the mount, and only one signaling behavior, soft songs (low-amplitude songs that song sparrows tend to sing from close range), was significantly associated with a subsequent attack. None of the other signaling behaviors, including type matching, was associated with whether or not the subjects attacked the mount subsequently (Searcy et al., 2006). If type matching does not predict successfully that an attack is impending, how can it be a threat signal?

There are at least two possible answers. First, this case may simply be another one of the differences between eastern and western song sparrow populations that we alluded to earlier. Some populations of eastern song sparrows, including the Pennsylvania population that Searcy and colleagues studied, show very limited song sharing (Hughes et al., 1998, 2007), and it is possible that the signaling code of Washington song sparrows does not apply to Pennsylvania song sparrows where song sharing between neighbors is uncommon —hence type matching and repertoire matching would not be possible most of the time. However, a subsequent playback experiment we carried out in our Washington population also failed to confirm that type matching was a reliable predictor of an impending attack (Akçay et al., 2011). Thus, although population differences may be part of the answer, they do not seem to be the whole answer.

The second possible answer is that type matching, while a threat signal and thus predicting escalation, is a long-distance, low-level signal that is given early in a sequence of aggressive interaction, well before an actual physical fight. If it were true that type matching is a low-level threat signal, it generally would not be an appropriate signal when the intruder is already in the middle of the territory, having boldly gone where he really should not have. In other words, in the face of such a high-intensity threat, the subject should not be expected to use a conventional signal that generally functions as a long-distance, early-stage signal across territory boundaries.

We therefore carried out a two-stage experiment to assess the reliability of type matching early in the interaction in predicting higher-level threats and eventual attack. In such an experiment, as proposed first by Beecher, Campbell, Burt, and colleagues (2000), the playback of a matchable song would start at the boundary in the first stage, eliciting a type match or a nonmatch. At the second stage the playback would be moved immediately to inside the territory of the subject, a clear escalation. Adding to the mix a taxidermic mount that is coupled with the playback at the center would also allow the subjects to attack the intruder. With this two-stage design, we can then ask whether type matching early in the trial will result in higher levels of aggressive signaling and attack.

Our prediction was that type matchers at the boundary would be more aggressive at the center, giving more soft songs and wing waves (fluttering one wing at a time such that the bird does not actually take off from the branch) and attacking at a higher rate. This prediction, however, had to be more refined given what we already knew about type matching. First, we knew from previous experiments that birds sometimes switch off type in response to being type matched (Burt et al., 2001). This could happen for a variety of reasons, including the unwillingness of the bird to engage in a fight just then because of conflicting activities such as feeding and mate guarding or because of assessing the opponent as a higher-quality male than himself. Whatever the cause, if a bird initially type matches but switches off type immediately after the playback moves to center, he is predicted to not show high levels of aggression. On the flip side, a bird might fail to type match the playback at the boundary for reasons other than unwillingness to escalate—the bird might perceive the boundary playback as simply not a serious enough threat, or he might be too busy with other activities (such as feeding young). However, we predicted that these birds would switch to a type match once the threat became unambiguous, that is, when the playback moved to the center. Taking into account these possibilities we predicted that birds who (1) type matched at the boundary and stayed on type when the playback moved to center or (2) did not type match at the boundary but type matched as soon as the playback moved to the center would escalate to high-intensity threat signals and eventually attack. We called these birds type matchers. In contrast, we predicted that birds who type matched at the boundary but switched off type once the playback moved to the center ("switchers"), that is, who deescalated by singing conventions, would behave less aggressively. Finally, birds that did not type match the playback ("nonmatchers") either at the boundary or at the center were also predicted to show lower levels of aggression. These predictions are summarized in Figure 2.8.

The results were largely in line with our predictions. As predicted, we found that type matchers were more aggressive than either the switchers or the nonmatchers, and all but two of them (15 out of 17, 88.2%) ended up attacking the mount. In contrast, attack frequencies for the switchers and nonmatchers were 50 percent and 52.2 percent, respectively, a significant difference. This was the first clear evidence that type matching as an early threat signal is predictive of an attack later on.

There were, however, some notable exceptions. Mentioned above was the fact that exactly half of switchers (four out of eight) also ended up attacking the mount. We predicted that switchers would only include birds that deescalated after an initial threat; that is, they would be "bluffers" in the sense

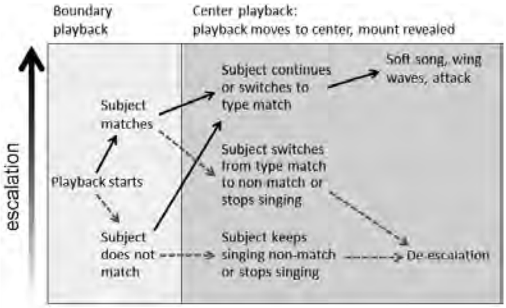

Figure 2.8. The hierarchical signaling hypothesis in the context of the experiment of Akçay et al. (in press). The design has two phases. In the first phase, song is played from the subject's territory boundary. In the second (escalation) phase, the playback switches to the center of the territory and the mount is revealed. When the bird hears a song from his territory boundary, he may or may not consider it seriously threatening. If he does consider it threatening, according to the hierarchical signaling hypothesis he should type match and should continue to type match once the escalation occurs (breaking off the type match is considered a deescalation). If the bird does not consider song from the boundary threatening enough to warrant a type match, by hypothesis he will certainly consider the escalation into his territory threatening, and he should type match at this point, that is, soon after the escalation. The common denominator of these two patterns is that the bird should type match in the short period following escalation. The results are consistent with this prediction with the interesting exception of "undersignalers"—birds who attack with little or no signaling (discussed in text).

that they would threaten but not back up their threat with action once the opponent escalates. We were wrong on this count—half the birds we considered switchers were actually fast-escalating birds who, after type matching at the boundary, switched off type but directly into soft song and wing waves and ended up attacking the mount. All in all, only 4 birds out of a total of 48 subjects (8.3%) could be considered bluffers, that is, birds that type matched initially but failed to back up the threat signal with action subsequently.

Another notable exception was that about half of the nonmatchers (12 out of 23 birds) also attacked the mount. This result suggests that sometimes song sparrows just forgo the early threat signals and go for an attack. Indeed, there were even some birds who attacked without a single soft song or wing wave, both signals of aggression we found to be independently predictive of attack. In other words, some birds seemed to forgo aggressive signaling, opting for a strategy of undersignaling. The presence of these "strong, silent types" is puzzling all the more because the signals in question—type matching, soft song, and wing waves—are all cheap to produce. Nonetheless, it seems clear that a good portion of birds that are otherwise very aggressive and attack the mount in this experiment were not engaged in extensive signaling. Undersignaling in these cases would decrease the reliability of the signal in question. But here, the problem is not so much ***deceptive signaling*** (i.e., signaling threat without the intention of backing it up with action), but the reverse problem of not giving threat signals when the aggressive intent in fact is there. One possibility is that these birds rely mostly on other behaviors to warn the opponent of an impending attack, such as a direct and quick flight towards it, flying around the opponent intently, and so on. These behaviors would not be considered ***signals*** per se because they did not evolve for a signal function (Otte, 1974) but nevertheless could provide information to the receiver regarding the likelihood of an impending attack.

In summary, these results indicate that type matching is an early threat signal that would be followed with higher-level threat signals such as soft songs and wing waves. It would therefore seem to be beneficial for a bird to be able to type match his opponents. To do that, however, the birds need to share at least one song type, and, presumably, the more songs a bird shares with likely neighbors the better. This brings us to the other and equally important aspect of song that we studied: song learning.

THE RELATIONSHIP OF THE SONG COMMUNICATION SYSTEM TO THE PROCESS OF SONG LEARNING

As reviewed above, song is the mechanism by which male song sparrows communicate with their male neighbors. Song is important as well in communication with females, but our studies have focused mostly on the male-male side of the equation (for perspective on the female side, see O'Loghlen & Beecher, 1997, 1999). In this final section, we consider the mutual fit of two processes: (1) the process we have been describing—how song is used between territorial song sparrows in our population, and (2) the process of song learning in these birds. We focus on the mutual fit because at present we cannot really determine the direction of causality in this relationship. That is we cannot say whether shared songs are the key to this communication system because song sharing is an inevitable consequence of learning the songs of your neighbors, or whether the process of song learning has been shaped by natural selection so that song sparrows learn songs they will share with their ultimate neighbors. More generally, it is remarkable that the function of song learning, a fundamental and defining characteristic of the more than 4,000 species of oscine passerines (songbirds), still remains largely a mystery after years of intensive study (Beecher & Brenowitz, 2005). Nevertheless, in this section we try to identify the possible advantages male song sparrows in our population may derive from their ability to learn their songs.

What We Know about Song Learning in Western Song Sparrows

We have carried a variety of field studies and lab studies on song learning in our population of song sparrows (Beecher, Campbell, & Stoddard, 1994; Beecher et al., 2007; Nordby et al., 1999, 2000, 2001, 2002, 2007; Burt et al., 2007; Nulty et al., 2010; Templeton et al., 2009; Templeton, Campbell, et al. 2012;Templeton, Reed, et al. 2012; Akçay, Campbell, et al., in preparation). We summarize these results here as "rules of song learning" for this population.

Rule 1—Copy songs of conspecific singers. In nature, song sparrows copy only song sparrow song in the field, although the occasional copy of a song or song element of a Bewick's wren (*Thryomanes bewickii*; personal observation) or white-crowned sparrow (*Zonotrichia leucophrys*; Baptista, 1988) are reported. In the lab, song sparrows readily copy swamp sparrow (*Melospiza georgiana*) song (Marler & Peters, 1988), so it would appear their failure to copy ***heterospecific*** song in the field (except for on the odd occasion) implies a mechanism for selecting conspecific models.

Rule 2—Complete song learning by the first spring. Because adult males (potential song tutors) in our population typically remain on their territories from one year to the next unless they die in the interim, it is difficult for us to determine from field data exactly when the young bird memorized his songs. But combining our lab studies with our field studies, we conclude that young song sparrows usually memorize their songs in the several months following dispersal from the nest (May, June, and July being the prime months for most birds), that is, in the traditional lab-determined ***sensitive period***, roughly the second and third months of life (Marler & Peters, 1987). However, our lab studies indicate that some birds will memorize new songs they hear for the first time the following spring, possibly because they did not memorize enough songs the previous summer (Nordby et al., 2001; Nulty et al., 2010; Templeton, Burt, et al., 2012), a pattern that has been demonstrated as well in marsh wrens (*Cistothorus palustris*; Kroodsma & Pickert, 1980). Although most memorization occurs in the natal summer, extensive modification of the song repertoire continues into the following spring—comparison of a bird's song repertoire in early spring (e.g., January) with his final repertoire in March or April typically reveals that he has modified his song repertoire by dropping songs, combining songs, and rearranging elements in songs. However, birds do not change their song repertoires after their first breeding season (Nordby et al., 2002).

Rule 3—Copy song types completely and precisely. Young song sparrows often develop near-perfect copies of the songs of their older neighbors. It is this fact that first made us realize that we could trace song learning in the field (when we began our field studies, almost all studies of song learning had been done in the laboratory). The song similarities can be striking, with the differences between tutor and student often being no greater than one normally sees in repetitions of the same song sung by one bird. In contrast, laboratory studies by Peter Marler and Susan Peters (1987, 1988) using recorded songs as the tutor stimuli found that while song sparrows copy song elements quite precisely, they frequently combine elements from different songs to form "hybrid" song types—songs made up of parts of different song types. That is, they often copy song elements but use them to improvise new song types.

We are still not sure to what extent this difference reflects differences in laboratory and field song-learning conditions (which of course are substantial), as opposed to differences in the eastern and western populations of song sparrows. The substantial differences in patterns of song learning shown by different songbird species, and in some cases by different populations of the same species (Brenowitz & Beecher, 2005), indicate that population differences cannot be dismissed as a possible explanation here. Indeed we have argued elsewhere that only careful ***common garden*** experiments can support or eliminate this hypothesis (Beecher, 2008).

Rule 4—Learn the songs of multiple birds. Usually it takes three to five song tutors to account for the young bird's entire repertoire of eight or nine song types. For example, in Cully Nordby and colleagues' study (Nordby et al., 1999), only 1 of the 41 subjects appeared to be a song "clone" of a single older bird. In the study by Çağlar Akçay and colleagues (Akçay, Campbell, et al., in preparation), only 1 of 43 subjects was a song clone. Nevertheless, about half the time the young bird learns the majority of his songs from one "primary" tutor (see Rule 7).

Rule 5—Learn from your neighbors. A bird's song tutors almost always turn out to have been neighbors in the young bird's hatching summer, and, if they survived the winter, the following spring (the young bird's first breeding season) as well. The young bird usually establishes his territory within the territorial range of his song tutors, often replacing a tutor that died. In the cases where the young bird does not establish his territory among his tutor-neighbors, the evidence suggests that he did not because he could not—because none of his tutors had died or because other young birds moved into this area. An example is shown in Figure 2.9 (note that it contains a larger-than-normal level of overwinter attrition of adult tutors).

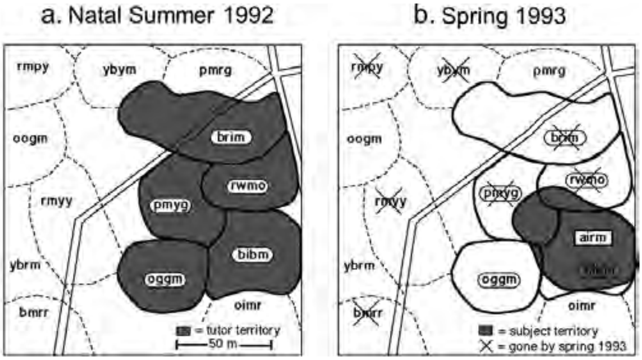

Figure 2.9. Diagram indicating song learning and territory establishment. (a) Territories of AIRM's tutors in his natal summer (1992). Adult birds (potential tutors) are shown by their color bands (four-letter codes) and their territories by dotted lines. The identified tutors of AIRM and their territories are shown by the dark hatching. (b) Territory of AIRM the following spring (1993), overlaid on the territories of summer 1992. Adult males who did not survive the winter are crossed out. Of the 13 adult birds shown, 8 out of 13 did not survive the winter; four out of AIRM's five tutors did not survive the winter. (This is an unusually high mortality rate—overwinter survival is typically 60 to 70%.) Note that AIRM established his territory in an area overlapping the former territories of three out of the four deceased tutors and next to his one surviving tutor (OGGM). The young bird shared songs with the surviving tutor and with other young birds that moved into that area as they had similarly learned songs of the area. (From Nordby et al., 1999. Reprinted by permission of Oxford University Press.)

Rule 6—Preferentially learn or retain song types of tutors surviving to your first breeding season. Birds often have song types that can be traced to tutors that were alive in the young bird's natal summer but died before the next breeding season. Nevertheless, they generally retain more songs of tutors who survive into the next breeding season than of tutors who do not. We refer to this late learning as late influence because it may not be *de novo* learning—these songs could have been memorized in the natal summer and retained because the bird continues to hear them the following autumn or spring. This would be the pattern hypothesized as typical by Douglas Nelson and Marler (Nelson, 1992; Nelson & Marler, 1994)—the young bird memorizes songs during a sensitive period in the natal summer and the following spring, retains some of these songs, and drops others on the basis of his social interactions with his territorial neighbors ("selective attrition"). We have recently compared the song repertoires of young song sparrows in the ***plastic song*** phase (late winter, early spring) and ***crystallized song*** phases and found that they do indeed retain songs that are more similar to those of their springtime territorial neighbors, while dropping some songs that are less similar (Nordby et al., 2007).

Rule 7—Pick a best tutor. Although the birds learn from multiple tutors (Rule 4 above), not all tutors contribute to the final repertoire of the bird equally. In rare cases, as mentioned above, the tutee's repertoire is a complete clone of one particular older bird. In other cases, the best tutor contributes only slightly more than the rest of the tutors and the repertoire is more or less made up evenly of songs from different tutors. But in most cases, the repertoire of the bird is skewed towards one particular tutor, who often is a neighbor. Nordby and colleagues (1999) found that on average half of the songs in a tutee's repertoire comes from the best, or primary, tutor. The best tutor is usually either a direct or once-removed neighbor that has survived into the first spring of the tutee.

Rule 8—Preferentially learn tutor-shared songs. As noted earlier, in our field population neighbors typically share a portion of their song repertoires, on average about two to four of their eight or nine song types. We have found that the young bird preferentially learns (or retains) song types shared by two or more of his tutors (Beecher, Campbell, & Stoddard, 1994; Nordby et al., 2000, 2001). There are several possible reasons that shared song types might be particularly salient, including (1) these types are heard more than unshared song types, (2) the "same song" is being sung by several birds, and (3) they are heard more often in countersinging interactions than are unshared songs. We consider the last possibility further below.

One possible function of the learning preference for tutor-shared songs is that it represents a ***bet-hedging*** strategy to guarantee that the young bird has song types he will share with his neighbors in his first breeding season. If instead the bird learned tutor-unique songs, he would have songs specialized for these particular tutor-neighbors (i.e., would share these songs with one neighbor only). But these specialized songs would be good only until the tutor died or moved, whereas a shared song would be good until all the birds having it in the neighborhood died or moved, and probably even longer because other young birds moving into the area would also preferentially learn shared types.

Rule 9—Individualize your song repertoire. The rules so far can be interpreted to fit the following overall rule: *Learn songs that you will share with your neighbors in your first breeding season*. There is, however, an important exception to that rule (Nordby et al., 2007). In the transition from plastic song to final crystallized song, the young bird often modifies a song so that it actually becomes a poorer match to the model song of the putative tutor and to similar songs of his present neighbors (who may or may not include the tutor).

We interpret this as the bird's "individualizing" his song, much like a pop singer putting his or her own personal touch on an old standard. The song may still be perceived by the birds as a shared song (even if it perhaps no longer meets our criteria for a shared song), while at the same time being perceived as his particular version of that song type. Thus the bird gets to have songs that are both shared with his neighbors and yet unique to him. Our many playback experiments and lab perception experiments (e.g., Stoddard et al., 1992; Horning et al., 1993; Beecher, Campbell, & Burt, 1994) have indicated that birds can discriminate among rather different versions of one particular song type while recognizing their similarity. Thus individualizing a song, as song sparrows often do, may simply stamp the song as the bird's own (strengthening individual distinctiveness) while maintaining his ability to use it as a shared song in the communication system.

Rule 10—Social interaction is crucial for song learning. There is ample evidence from our lab studies of song learning and from many others as well that song learning is enhanced if the young bird experiences social stimulation from live singing birds; indeed these "live tutors" are generally much more effective than simple playback of recorded song (see review in Beecher, 2008). In several of our lab studies with live tutors, we found that social interaction was critical but that the tutee did not necessarily need to directly interact with the tutor or even see him (Nordby et al., 2000, 2001; Beecher et al., 2007). In these experiments birds often learned as well or even better from tutors they could hear but not see and from tutors who interacted not with them but with some other bird. That song learning might require a social interaction context without necessarily involving direct interaction between tutee and tutor was confirmed in a field experiment—we found that young song sparrows in the song-learning phase found playback simulating an interaction between two adult singers much more attractive than playback simulating a solo singer (Templeton et al., 2009). In further field experiments, we found that adult song sparrows are surprisingly tolerant of young, recently fledged birds, who would often sit close to the adult bird while it interacted with a simulated intruder (mount plus playback; Templeton, Campbell, et al., 2012).

QUESTIONS THAT REMAIN

As the review above makes it clear, we have very detailed information on the pattern of song learning in song sparrow and the use of song in interactions between adult males. Very interesting questions still remain, however. The most important of these is the role of social interactions in tutor choice. Although we have very good evidence from lab studies that social interactions between the tutee and tutors as well as between potential tutors matter, the nature of the interactions that can be studied in the lab is very narrow and inherently unnatural. For instance, in the field, a young bird can simply move off to get away from an escalating situation, whereas in the lab he is stuck in a cage. Therefore, the nature of social interactions is best examined in the field.

One question we are currently pursuing is the question of why song sparrows choose one particular male as their primary tutor and why they choose this particular individual rather than another. In other words, why is the repertoire of the young song sparrows so highly skewed towards a single male, and what makes that male special?

One hypothesis is that birds skew their repertoire towards the primary tutor because it helps them negotiate their boundaries with this particular male. Establishing a territory is a costly affair, which usually takes persistence on the part of the challenger (Arcese, 1987, 1989), and once a bird establishes a territory the boundaries still need to be negotiated. In principle, any negotiations with a neighbor may be costly, but some neighbors might pose a particularly strong challenge because they are more aggressive. Indeed, there is evidence that in song sparrows (as in other animals) there are individual differences in aggression that are stable over time (Hyman et al., 2004; Akçay et al., 2013), and neighbors respond more strongly towards neighbors with more aggressive personalities (Hyman & Hughes, 2006).

Aggression may have several effects on song learning. Most simply, a young bird establishing his territory may have to engage in more interactions with an aggressive neighbor and as a result may learn his songs simply as a by-product. Alternatively, learning the songs from an aggressive neighbor may be beneficial for the young bird. Recall that song sparrows possess a complex long-range signaling system that relies on using shared songs in aggressive interactions before these escalate into close-range interactions that may involve physical fights. If it is true that some neighbors are more aggressive than others, it may be beneficial for a young bird to optimize his repertoire for use against these neighbors by learning his songs primarily from these males. Under this hypothesis, aggressive tutors are predicted to be better tutors.

A second, alternative hypothesis is that birds choose their tutors not based on their aggressiveness but rather on the basis of their dear enemy potential (Akçay et al., 2009, 2010). Under this hypothesis, tutees and primary tutors are setting up an (at least partially) cooperative relationship that may benefit each of them, and sharing songs facilitates their coordination. In other words, tutees learn their songs not from their “nasty neighbors” who are particularly aggressive towards them but from neighbors with whom they are setting up a dear enemy relationship. This hypothesis might be termed the Mr. Chips hypothesis after the beloved schoolteacher in the movie *Goodbye, Mr. Chips*.

A cooperative relationship between a tutor and a tutee should entail the tutor and tutee showing reduced aggression towards each other and perhaps even engaging in cooperative territory defense. We have found that song sharing in our population is correlated positively with territory tenure in song sparrows (Beecher, Campbell, & Nordby, 2000), suggesting that there is indeed potential for a cooperative relationship between a tutee and his primary tutor. To the best of our knowledge, however, no one has tested this hypothesis in song sparrows or any other songbird.

We are currently in the process of testing these two hypotheses regarding the role of social factors in tutor choice. Our preliminary results suggest that the aggression hypothesis is not supported in song sparrows. In a field study where we quantified stable individual differences in aggression (i.e., "aggressive personality") of almost half of the potential tutors in our study site, we found no effect of tutors' aggression on whether or not they were selected as tutees by the young males establishing their territories that year (Akçay, Campbell, et al., in preparation). This result suggests that aggression does not play a significant role in tutor choice of song sparrows. We are also planning experiments to test the Mr. Chips hypothesis.

CONCLUSION

Song sparrows have proved themselves a fruitful model system for investigating central questions in animal communication: those of reliability, social dynamics, and development. In this chapter we have tried to integrate the various lines of research from our laboratory on this fascinating system. We have gained many insights into the function and development of song repertoires in song sparrows and see many more fruitful avenues of research opening up.

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