Function and Mechanisms of Song Learning in Song Sparrows*

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DEDICATION

*Dedicated to my colleagues in the song sparrow research over the years (in order of appearance): Phil Stoddard, Liz Campbell, Patti Loesche, Cindy Horning, John Burt, Michelle Elekonich, Cully Nordby, Adrian O'Loghlen, Chris Hill, Suzanne Bard, Brendan Reeves, Tim Billo, Chris Templeton, and Caglar Akcay.

I. INTRODUCTION

A. BACKGROUND

The use of elaborate acoustic vocalizations, or song, in intraspecific communication is common in a wide variety of animal groups (Searcy and Andersson, 1986). In the oscine passerines (songbirds), song has an additional, intriguing aspect: it is learned. By present estimates, vocal learning has evolved independently in the birds, cetaceans, bats, and primates, and within the birds, independently in the songbirds, hummingbirds, and parrots (Jarvis, 2004). From the evolutionary point of view, the songbirds are particularly interesting because of the amazing variety of song-learning patterns that have been discovered within this group of 4000-odd species (Beecher and Brenowitz, 2005; Kroodsma, 1988, 1996). Within the primates, on the other hand, vocal learning appears to be confined to a single species, humans, and its presence in our species is the second reason for the fascination with song learning in the songbirds: its many parallels with human language learning. The parallels first recognized were: an early sensitive period, a perceptual filtering mechanism tuned to species communication signals, the key role of auditory feedback in normal development, a

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temporal separation between sensory and motor learning, and a subsong or babbling stage (Marler, 1970a; Nottebohm, 1970). These parallels have helped stimulate the study of the songbird neural song control system, which has become a major vertebrate model system for the study of neural plasticity (Doupe and Kuhl, 1999; Jarvis, 2004; Konishi, 1985; Marler, 1991; Nottebohm, 1984).

In most songbirds, song functions in the contexts of intrasexual competition and mate attraction. In most territorial temperate-zone passerines, only males sing and the major intrasexual context is the defense of the territory (review in Catchpole and Slater, 1995) with song functioning as a long-distance signal to ‘‘post’’ the territory and to communicate with neighbors in negotiating territorial boundaries. I will confine my discussion in this chapter to the case where only the male sings, but for more on cases where the female sings as well, see the recent review by Riebel (2003).

Evolutionary questions about song learning in songbirds focused originally on the adaptive advantages of learning versus not learning song, that is, on the origin of song learning in the oscine line (Nottebohm, 1972). As comparative studies of songbirds have accumulated, however, the focus has shifted to the evolution of different song-learning programs, the inferred genetic-developmental programs underlying particular patterns of song learning observed in a species, or a race or a population of a species (Beecher and Brenowitz, 2005; Kroodsma, 1978, 1983, 1996; Marler and Peters, 1988a; Nelson, 1999; Slater, 2003). The song-learning program specifies how learning proceeds and the critical features of the learning environment, for example, how long the sensitive period stays open; how many songs the bird keeps for his final repertoire; whether the bird imitates tutor songs or improvises on them, or invents new songs; whether the bird requires early exposure to conspecific song; how constrained the bird is to copy only songs that fit species-specific parameters; the key social variables to attend to; and so on.

B. Social Factors in Song Learning

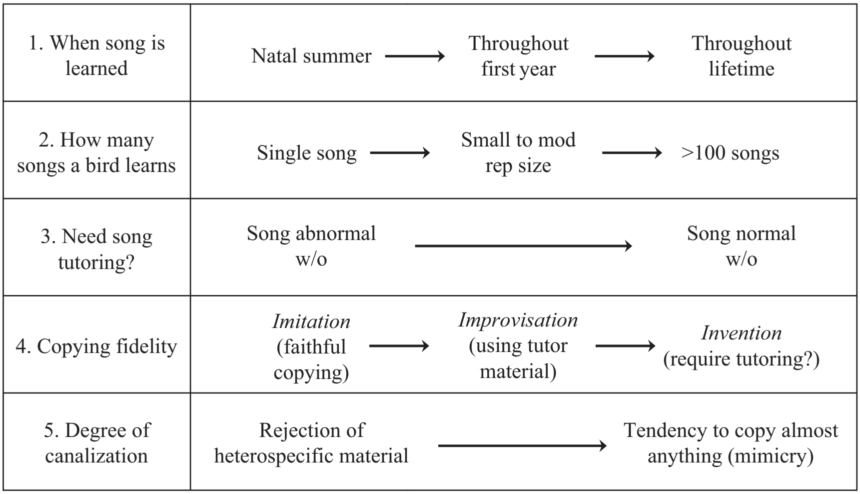
In this chapter, I focus on social factors in song learning. Early studies of song learning in the songbirds explicitly excluded social factors. There were both theoretical and experimental reasons for doing so. The original theoretical conception of song learning was derived from the classical ethological concept of imprinting, translated into the song-learning context by Thorpe (1958) and then fully developed in the experiments of Marler and his colleagues (e.g., Marler, 1970b). By analogy to the classical imprinting studies, it was supposed that the key stimuli for song learning would be very basic, processed by species-specific filtering mechanisms, and that learning would occur during an early ‘‘sensitive period.’’ This view provided the rationale for the *tape tutor* experiment, in which all aspects of the species- and population-typical song-learning context were removed except song. Besides fitting the theoretical view, the tape tutor experiment also indisputably provided more experimental control than would be possible were actual birds the song tutors. From this spartan experimental paradigm have come 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 (sometimes referred to as the ‘‘innate template’’). In his classic series of tape tutor experiments, Marler (1970b) showed that to develop normal song, a white-crowned sparrow male must hear conspecific song during an early sensitive period (roughly the second month of life); the bird will reject heterospecific song heard during this period, as well as conspecific song heard after the sensitive period. The tape tutor paradigm has generated most of what we know about song learning, and has been particularly valuable in identifying the sensory mechanisms that guide and constrain it (e.g., Soha and Marler, 2000, 2001).

Workers in the field became aware of the importance of social factors in song learning, however, with the discovery that birds learned more readily from live tutors than from tape-recorded song (Baptista and Petrinovich, 1984, 1986; Chaiken *et al.*, 1993; Clayton and Pröve, 1989; Cunningham and Baker, 1983; Kroodsma and Pickert, 1984a,b; Kroodsma and Verner, 1978; Nicolai, 1959; Payne, 1981; Price, 1979; Rice and Thompson, 1968; Thielke, 1970; Waser and Marler, 1977). Moreover, some of the rules of song learning derived from tape tutor studies appeared to bend, if not break, when the song tutors were actual birds. For example, whereas tape tutor studies had indicated that the sensitive period for white-crowned sparrows closes at ~50 days, and that heterospecific songs are uniformly rejected (Marler, 1970b), Baptista and Petrinovich (1984, 1986) showed that if a young white-crowned sparrow was exposed to a tape tutor through 50 days 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 he were a heterospecific tutor. Consider another example: In our study species, the song sparrow, young birds stop learning new songs from tape tutors in their natal summer by the time they are 3–4 months old (Marler and Peters, 1987), whereas they continue to learn new songs from live tutors into the fall and perhaps the following spring, when they are 5–9 months old (Nordby *et al.*, 2001). This difference, like many of the conflicting results from live and tape tutor experiments, has a significant confound and thus an alternative interpretation; in this particular case, the critical confound may be with differences in the song-learning programs of eastern and western song sparrows (discussed below in Section D). But despite such problems of interpretation and considerable debate (Baptista and Gaunt, 1997; Nelson, 1997, 1998), there is consensus on the point that ‘‘the social stimulus of a live adult is a more potent stimulus during song development than is the presentation of songs through loudspeakers alone’’ (Casey and Baker, 1993, p. 723).

While the live versus tape tutor contrast inevitably suggested the importance of social factors, the results of the tape tutor experiments themselves, especially the studies of Marler and Peters on ‘‘overproduction’’ in swamp sparrows, have provided additional motivation to search for social factors. In particular, Marler and Peters’ (1981, 1982a,b) finding that a swamp sparrow memorizes (and subsequently sings during the plastic song phase) more songs than he keeps for his final repertoire (overproduction) highlights the question: How does the bird *select* his final songs from the many he has heard? And this leads naturally to the question concerning the natural song-learning context: How does the bird choose his song tutors?

Finally, field studies have also provided a major impetus to the study of social factors. Although field studies cannot provide the experimental control of a laboratory study, they naturally bring into focus the social variables that are controlled out of laboratory experiments. To the question of *when* song learning occurs, field studies have added the questions of *where* and *from whom*, and have given a new context for the questions of *how many, which ones, and how accurately* (Kroodsma, 1978). Researchers doing the first field studies on song learning noted that learning appeared to occur later than indicated by the classical tape tutor studies, post- rather than predispersal, so that birds wound up learning songs not from their father and birds in the natal area, but from birds in the area where they would breed, often their neighbors of their first breeding season (e.g., Bewick’s wrens, Kroodsma, 1974; saddlebacks, Jenkins, 1978; white-crowned sparrows, Baptista and Morton, 1982; indigo buntings, Payne, 1982). Although this interpretation has been disputed (for reviews of this dispute, see Kroodsma *et al.*, 1984; Payne and Payne, 1997), these field studies stimulated attempts to incorporate social factors into accounts of song learning. The field studies of our group on song sparrows (Beecher *et al.*, 1994b; Nordby *et al.*, 1999, 2002, 2007) have also pointed to the importance of social variables, and will be considered in detail in Section III.

Despite the problems raised by field studies and by experiments with social tutors, the basic findings of the classical tape tutor experiments have not yet been firmly contradicted in any species. In particular, although the sensitive period for song learning may extend much further into the first year for some species than was originally thought, for no species does it appear to be true that song learning is equally possible or equally likely at all points during the bird’s life. Moreover, even if a powerful heterospecific social tutor can overcome it, the preference for conspecific song invariably found in tape tutor experiments does suggest some form of tuning for conspecific song. Nevertheless, comparative studies of songbird species have revealed an amazing diversity in song-learning patterns, both between species and between different populations of the same species, and this diversity should warn us not to take any particular pattern of song learning, for example, that shown by white-crowned sparrows, as "typical" or "fundamental" (reviews in Beecher and Brenowitz, 2005; Catchpole and Slater, 1995; Kroodsma, 1978, 1983, 1988, 1996). For example, in contrast to the "classic" song-learning pattern of the white-crowned sparrow, song learning in some oscines occurs long after the first few months of life, and indeed a bird may add songs throughout the lifetime; individuals may learn heterospecific songs in some circumstances; song learning may consist more of invention and improvisation than of simple imitation; the memorization and production phases of song learning may overlap extensively; song may develop apparently normally in the absence of any song tutoring; and so on (Beecher and Brenowitz, 2005). Figure 1 summarizes some of the important dimensions of variation in the song-learning programs of songbird species.



1. When song is learned	Natal summer	→	Throughout first year	→	Throughout lifetime
2. How many songs a bird learns	Single song	→	Small to mod rep size	→	>100 songs
3. Need song tutoring?	Song abnormal w/o	→			Song normal w/o
4. Copying fidelity	*Imitation* (faithful copying)	→	*Improvisation* (using tutor material)	→	*Invention* (require tutoring?)
5. Degree of canalization	Rejection of heterospecific material	→			Tendency to copy almost anything (mimicry)

FIG. 1. Major dimensions on which the song-learning programs of songbird species differ. (1) When song is learned or how long the song repertoire is modified: from a sensitive period early in life to throughout the lifetime. (2) How many songs a bird learns: from a single song to over a thousand (with small to moderate repertoire sizes being the rule). (3) Effect of isolation from song in early life: from birds that produce normal species song to birds that produce grossly abnormal song. (4) Copying fidelity: from imitation (faithful copying of tutor song) to improvisation (using tutor material) to invention (which may or may not require song tutoring). (5) Degree of canalization: from rejection of heterospecific material to ability to learn almost anything (mimicry).

A nice example of a difference in song-learning programs was provided by a comparison of song learning in two closely related emberizine sparrows by Marler and Peters (1988a,b). Using the tape tutor method, they showed that song sparrows will sometimes copy heterospecific elements, especially if they are embedded in song sparrow like syntax, whereas the congeneric swamp sparrows will not, regardless of the syntactical context. This example is but one of many illustrating the fact that the different songbird species show many different patterns of song learning. Although we are a long way from a comprehensive account of song learning in the songbirds, in the end such an account will have to deal with this diversity.

II. Studies of Social Factors in Song Learning

Despite the gathering consensus on the importance of social factors in song learning, we have little understanding of *how* social variables shape song learning. The numerous comparisons of live versus tape tutors mentioned above are usually indirect (often across different studies), and only a very few studies have actually attempted to analyze social factors. As Nelson has pointed out, it is not at all clear what precise aspects of social stimulation influence song development, and indeed even whether the effects are ‘‘truly social’’ (Nelson, 1997). A major goal of our research group over the past 20 years has been to uncover and analyze the social factors in song learning in the song sparrow (*Melospiza melodia*). Before turning to that research, in this section, I consider other research on this topic, and in the following section, several new theories about how social factors may operate in song learning.

Researchers have taken two rather different approaches to analyzing the role of social factors in song learning. In one approach, researchers manipulate large-scale social context settings, typically in large aviaries. The best example of this kind of research comes from the West-King group studying cowbirds, and the Eens and Hausberger groups studying starlings (e.g., Eens, 1997; King *et al.*, 2005; Poirier *et al.*, 2004). The usual manipulation consists of setting up different kinds of social groups, and then contrasting differences in song learning in these groups. For example, the comparison can be between subjects housed with adult males versus those housed without, or housed with females from the same population versus females from a different population (King *et al.*, 2005; White *et al.*, 2002). The conclusions that come from these studies tend to be rather broad-brush, and often pertain to more general behavioral competencies. I do not attempt to summarize these studies in this chapter.

The other approach has been more analytic, using simpler social situations and trying to isolate key variables. This approach has produced few conclusions to date, probably because there are only a small number of social variables one can actually manipulate when the song tutors are live birds. You can vary how close the tutor is to the subject, whether he is visible to the subject, whether the two can physically interact, and so forth, but you cannot manipulate the actual behavior of the tutor (including his singing) except in fairly gross ways (e.g., with a testosterone implant). To date, most of these studies have focused on one or another of the following four hypotheses.

According to the *Aggression hypothesis,* young birds learn more from aggressive song tutors. Payne (1981), for example, found that 1-year-old captive indigo buntings were more likely to copy songs of an adult they could interact with directly than those of an adult they could hear and see but not interact with directly. However, while aggression was observed, it was not isolated from other variables relating to social contact. Similarly, Clayton (1987) housed male zebra finches with two adult males from 35 days post-hatching on, and found that the subjects learned preferentially from the adult that showed more aggression toward them. On the other hand, Casey and Baker (1993) found that when aggressive adults were the only available song tutors, young white-crowned sparrows not only failed to copy their songs but also developed abnormal songs.

According to the *Contingency hypothesis,* the key element in social interactions is that the tutor song is contingent on some behavior of the young bird. Several studies have used a variation on the tape tutor design where an arbitrary response of the bird (e.g., a key peck) triggers song presentation. Despite some promising early studies, however, a recent replication study by Houx and ten Cate (1999) found no difference in the learning of contingent versus noncontingent song.

According to the *Visual Signal hypothesis,* it is the live tutor's visual presence that makes him more effective than the tape tutor. However, most of the studies that have actually manipulated visual exposure, while controlling other facets of social interaction, have failed to support this hypothesis. In the zebra finch, exposure to a visual model of an adult male paired with song playback does not enhance learning relative to exposure to playback alone (Bolhuis *et al.*, 1999). Moreover, zebra finch fledglings prevented from seeing by eye patches still learned from a tutor in the same cage (Adret, 2004). In the next section, I discuss our experiments indicating that the visual component is not critical in song learning for song sparrows. Finally, considering human parallels, it is worth noting that blind children learn language with no difficulty.

In summary, there is minimal support at the present time for any of these hypotheses about possible social factors in song learning, although the problem at this point is less an accumulation of negative evidence as it is a lack of evidence (negative or positive). In the next section, I consider three theories concerning social factors that are somewhat orthogonal to the hypotheses just considered.

III. Developing Theories of Song Learning

The tape tutor versus live tutor controversy can be viewed from another, purely theoretical angle. Although this is rarely discussed, the tape tutor and live tutor paradigms implicitly suggest different models of the nature of the song-learning process. The tape tutor paradigm implies that song learning is essentially a process of overhearing or *simple eavesdropping* on a singing adult. In contrast, the typical live tutor setup—with the young bird stationed close to a singing adult bird—implies that the fundamental process involves *direct interaction* of the older bird (song tutor) with the young bird. However, as Marler has noted (Marler and Peters, 1988b), both experimental setups are potentially ‘‘unnatural’’: We do not know if in nature the young bird learns from a song tutor who is singing solo and out of sight (as implied by the tape tutor design), or from a song tutor who is up close and interactive (as implied by the typical live tutor design), or, perhaps, in some other way altogether.

The major attempt to reconcile the conflicting views generated by the tape tutor and live tutor paradigms has been a theory proposed by Nelson and Marler (1994). According to this theory, song learning occurs in two phases. In the first phase of song learning, the young bird memorizes many songs during the natal summer, many more songs than he will ultimately keep for his final repertoire. In the second, ‘‘action-based’’ phase of song learning, typically occurring early in the following spring, the bird countersings with his new neighbors as he tries to establish a territory, and selects from his earlier- memorized songs those that best match the songs of the birds he is now interacting with. Thus, the Nelson–Marler theory incorporates the implicit models of both the tape tutor and live tutor paradigms: The early, memorization phase of song learning follows the ‘‘simple eavesdropping’’ model, while the later ‘‘action-based’’ phase conforms to the ‘‘direct interaction’’ model. Although the Nelson–Marler theory is consistent with the results of a number of laboratory and field studies (e.g., Nelson, 1992; Nordby *et al.*, 2007), to date, there is no direct field evidence concerning the nature of the social interactions that occur during the presumptive ‘‘action-based’’ learning phase (or for that matter, of those that may or may not occur during the presumptive ‘‘memorization’’ phase).

Here I propose a third model, based in part on recent research on *social eavesdropping* (Peake, 2005), which indicates an alternative way in which social interaction might affect song learning. The central idea is that the young bird learns by eavesdropping, not on solo singing, but on singing interactions between two or more birds. Recent field experiments on songbirds have shown that males base their decisions on whom to challenge and females base their decisions on whom to mate with on information about the dominance relationship of the singing males, information which they extract when eavesdropping on singing interactions (Mennill *et al.*, 2002, 2003; Naguib and Todt, 1997; Naguib *et al.*, 1999, 2004; Otter *et al.*, 1999; Peake *et al.*, 2001). In the species studied to date, song overlapping, song-type matching, and/or song leading seem to be the critical cues signaling dominance (Kunc *et al.*, 2006; Mennill and Ratcliffe, 2004; Naguib, 1999; Peake *et al.*, 2005). We hypothesize that young birds too may use information they extract from singing interactions they overhear to decide which songs to learn or retain; dominance would likely be one important dimension. The only field study to date that relates dominance to song learning is Payne's field study of the African village indigobird (Payne, 1985). He found that village indigobirds typically copied the song of the dominant bird in the area. Also relevant is the ''social modeling'' theory, as developed by Pepperberg, which suggests that observation by the young bird of communication interactions between individuals who have mastered the communication system may be critical for vocal learning (Pepperberg, 1985).

There is a second unique type of information a young bird could extract from the interactive singing (counter-singing) of two adults that he could not extract from solo singing of these same birds: contextual information relating to *singing rules* concerning the appropriate replies to particular songs in particular contexts. We discuss singing rules we have observed in song sparrows in Section IV.B below. In the study of bird song learning, the focus has always been on the learning of particular songs rather than the learning of how to use them, but the two processes may be intertwined. This is the case for human language learning of course, and the notion that this might be true for a songbird as well provides additional rationale for testing the Social Eavesdropping hypothesis. A key prediction of the Social Eavesdropping hypothesis—true regardless of whether dominance relationships or song reply rules are the key factor—is that a young bird who needs to interact with a new neighbor may select for his final repertoire not just the songs of that individual, but songs the young bird has heard other birds singing to that individual as well (or instead).

The previous discussion can be summarized in terms of three hypotheses about the social nature of song learning. These hypotheses are illustrated in Fig. 2. These hypotheses are not mutually exclusive, but they are eminently testable.

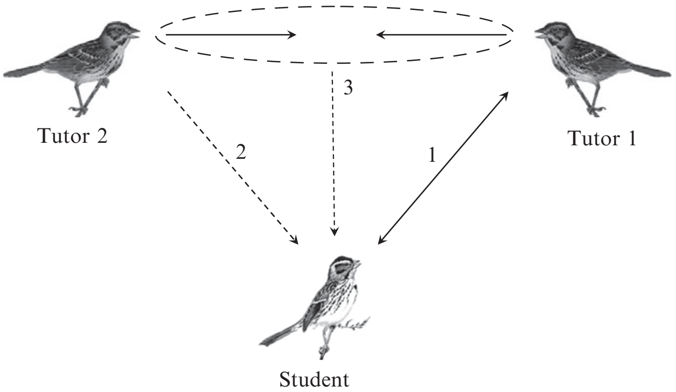


FIG. 2. Schematic representation of the ways in which the young bird could extract information for song learning, illustrating three different hypotheses concerning the song-learning process. Direction of arrowhead indicates the direction of singing. (1) *Direct Interaction:* The young bird learns songs of (or retains songs he memorized early that are most similar to those of) tutors he directly interacts with, counter-singing between tutor and student being critical. According to the Nelson–Marler theory, such interaction, usually involving song matching, is characteristic of the late phase of song learning. (2) *Simple Eavesdropping Hypothesis*: The young bird learns songs simply by listening to a bird sing, and no interaction is required. According to the Nelson–Marler theory, this pertains only to the early phase of song learning. (3) *Social Eavesdropping Hypothesis:* The young bird preferentially learns songs he overhears in counter-singing interactions between other birds. A young bird attending to both sides of the interaction can extract two unique types of information that he could not extract from solo singing of these same birds: contextual information relating to social dominance and song reply rules (see text).

IV. SONG FUNCTION AND SONG LEARNING IN SONG SPARROWS

A. RESEARCH PROGRAM

The goal of our research program has been to understand the role of song in the song sparrow's natural ecology and the function and development of song learning in this species. Song learning has traditionally been investigated in the laboratory under tightly controlled conditions. As noted earlier, the bulk of what we know about song learning comes from studies in which young birds are isolated from conspecifics at or near to hatching, and tutored by tape-recorded songs delivered from a loudspeaker. Clearly that approach is at the least incomplete if social factors play a role in song learning. On the other hand, our ability to understand the mechanisms of song learning is unlikely to be successful if we restrict ourselves to inference from field observations, no matter how good these observations may be. Because of the inevitable trade-offs between analytical rigor and ecological validity, a complete picture can be gained only by combining the differing perspectives of field and lab, and of observation and experiment. For this reason, in our research program, we have taken a wide range of approaches, including field observation, field experiments, ‘‘semi-natural’’ lab studies, and more controlled lab studies (Fig. 3). In the next sections, I summarize our major findings from these various studies.

B. Background

Our study species is the song sparrow (*Melospiza melodia*), a common species found throughout North America. A male song sparrow typically has 6–12 distinct song types in his song repertoire (Peters *et al.*, 2000). A typical song repertoire in our population is shown in Fig. 4. Female song sparrows do not sing (except under rare circumstances, see Arcese *et al.*, 1988). A song sparrow sings his song types with ‘‘eventual variety,’’ that is, he repeats songs of one type many times (a ‘‘song bout’’) before switching to a new type. In ‘‘free’’ singing (i.e., when the bird is singing solo, not interacting with another bird), a song sparrow uses the different types interchangeably and with approximately equal frequency, although his pattern of singing is different when counter-singing with a neighbor (see

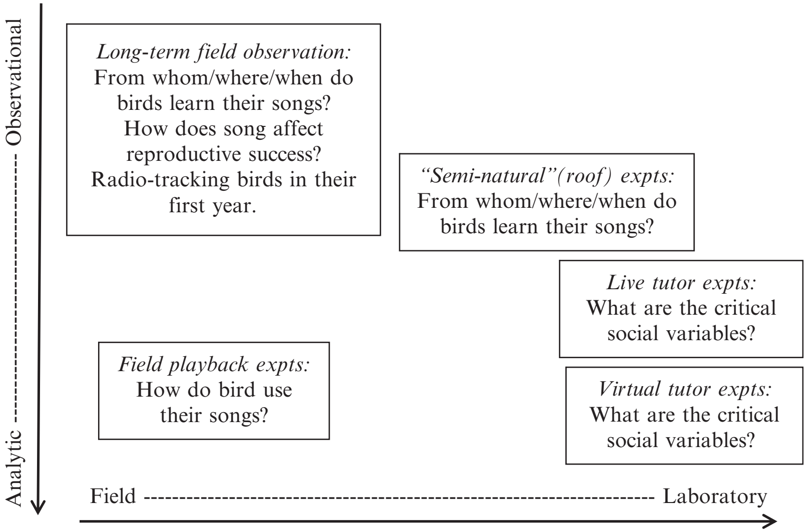


Fig. 3. A schematic representation of our research program. Note that field studies can be observational or experimental, and lab studies too can range from observational ‘‘semi-natural’’ studies to more analytic experiments.

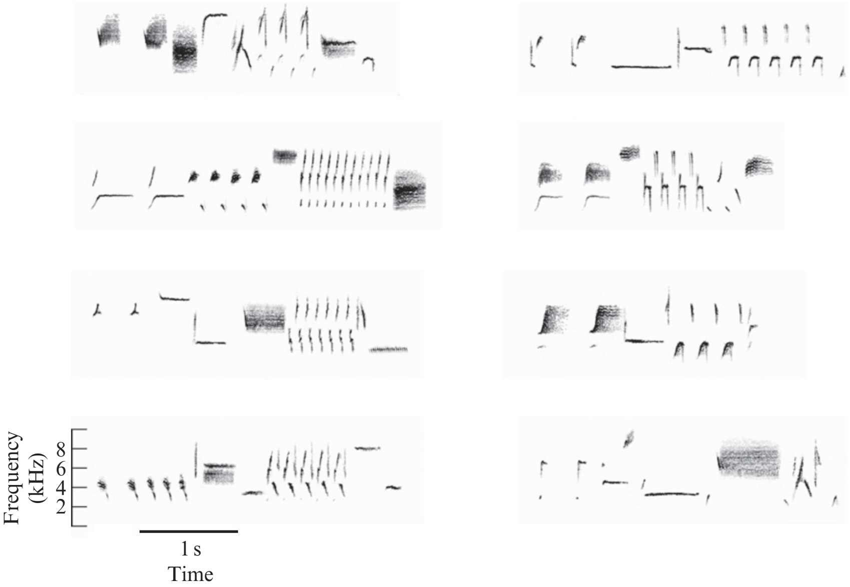


FIG. 4. The song repertoire of one male. Frequency (vertical) scale: 0–10 kHz, markers at 2 kHz intervals. Songs are 2–3 s long.

below). Within a bout of one song type, a song sparrow sings variations on the type, but this intra-type variation is small compared to inter-type variation, and a song type may be considered as a class of very similar songs (Fig. 5, Nowicki *et al.*, 1994; Podos *et al.*, 1992; Stoddard *et al.*, 1988). A particular song X is classified as belonging to song type class A rather than song type class B if (1) it is structurally or perceptual more similar to A; (2) the bird sings X in bouts of A rather than in bouts of B; and (3) in response to playback of song X, the bird responds with a song from the A class rather the B class.

Although the song types in an individual's repertoire are as distinct from one another as are the song types of different birds, as just suggested, neighboring birds will often share some of their song types. As we will see, these similar song types can be traced to a history of song learning, that is, one bird having learned from the other, or both having learned from a third bird, or some other history of song learning (the more links in the chain, the less similar the songs will be). Examples of song sharing are shown in Fig. 6 (for two neighbors) and Fig. 7 (for three neighbors). The song sharing in Fig. 6 is close enough that, for the three shared types shown, one of the birds was likely the song tutor of the other bird. Figure 7 shows several songs where the sharing is not so close, and illustrates that the criteria the investigator uses

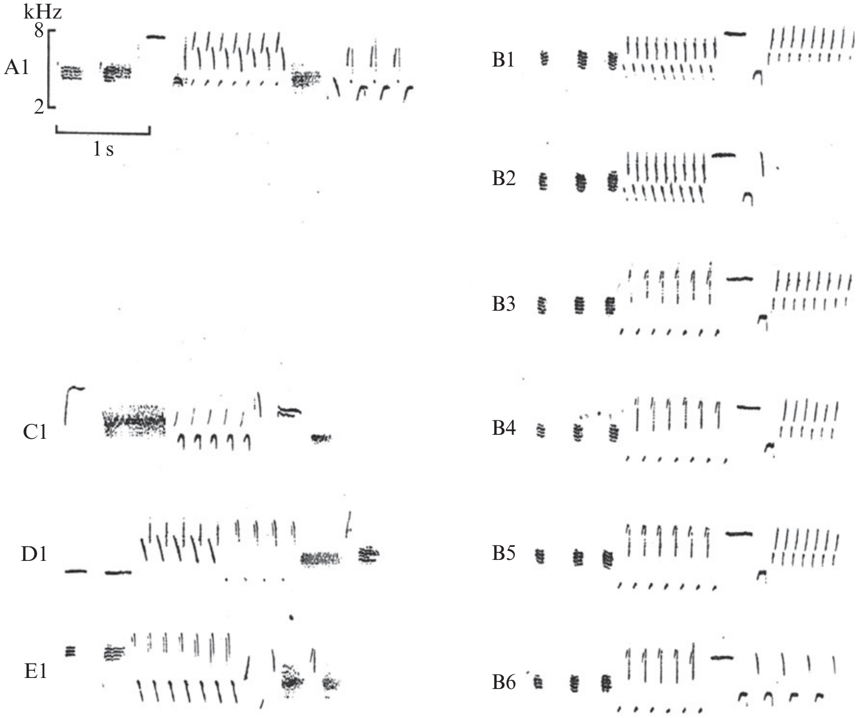


FIG. 5. A partial repertoire of one male illustrating the larger differences between types (contrast A through E) and the smaller differences among variations within a type (a natural sequence of 6 B variations is shown). Note that variations in the B's are mostly in the latter part of the song (typical): The terminal trill is dropped in B2, and replaced with a different trill in B6, and the middle trill is replaced with a different trill in B3. Other small changes can be detected, for example, in the number of elements in a trill.

to declare two songs ''shared'' are necessarily arbitrary. The ultimate criterion for sharing, and one that can be applied only on occasion, is that the two birds behave as if they perceive the songs as shared, as when they ''type-match'' each other with their shared songs (discussed in the next section).

Song sharing is very local, with birds more than four or five territories apart rarely sharing song types. This pattern of neighbor song sharing—which has been observed in many different songbird species (see Catchpole and Slater, 1995)—will occur when young birds learn the songs of the neighborhood into which they immigrate following natal dispersal. A young song sparrow usually begins singing subsong in the late summer or early fall, but does not sing adult-like song until the following spring. He

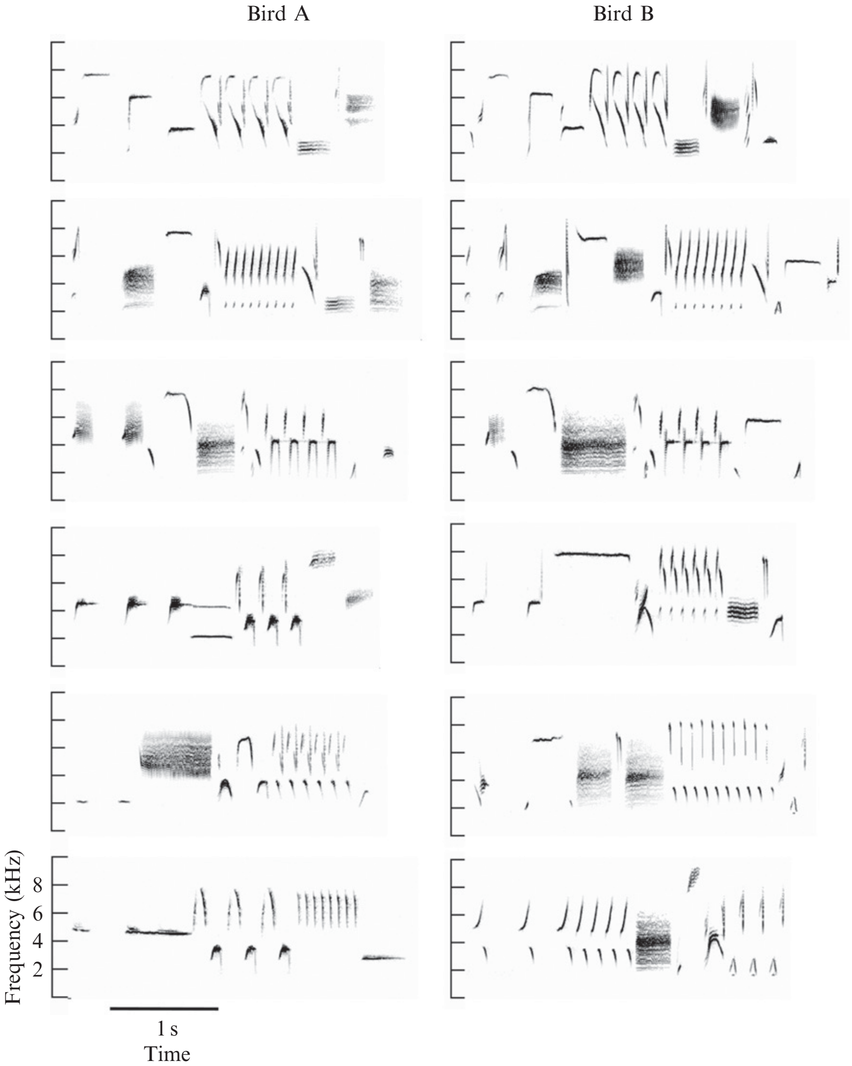


FIG. 6. Partial song type repertoires of two song sparrow subjects. Birds A and B were neighbors and shared the first three songs in their nine-song repertoires (33% sharing). The shared songs of birds A and B are shown in the top three rows, while six of their remaining unshared types are shown in the bottom three rows.

usually crystallizes his repertoire by early or mid March, shortly before the breeding season begins in earnest. He does not add or delete songs from his repertoire after his first breeding season (Nordby *et al.*, 2002).

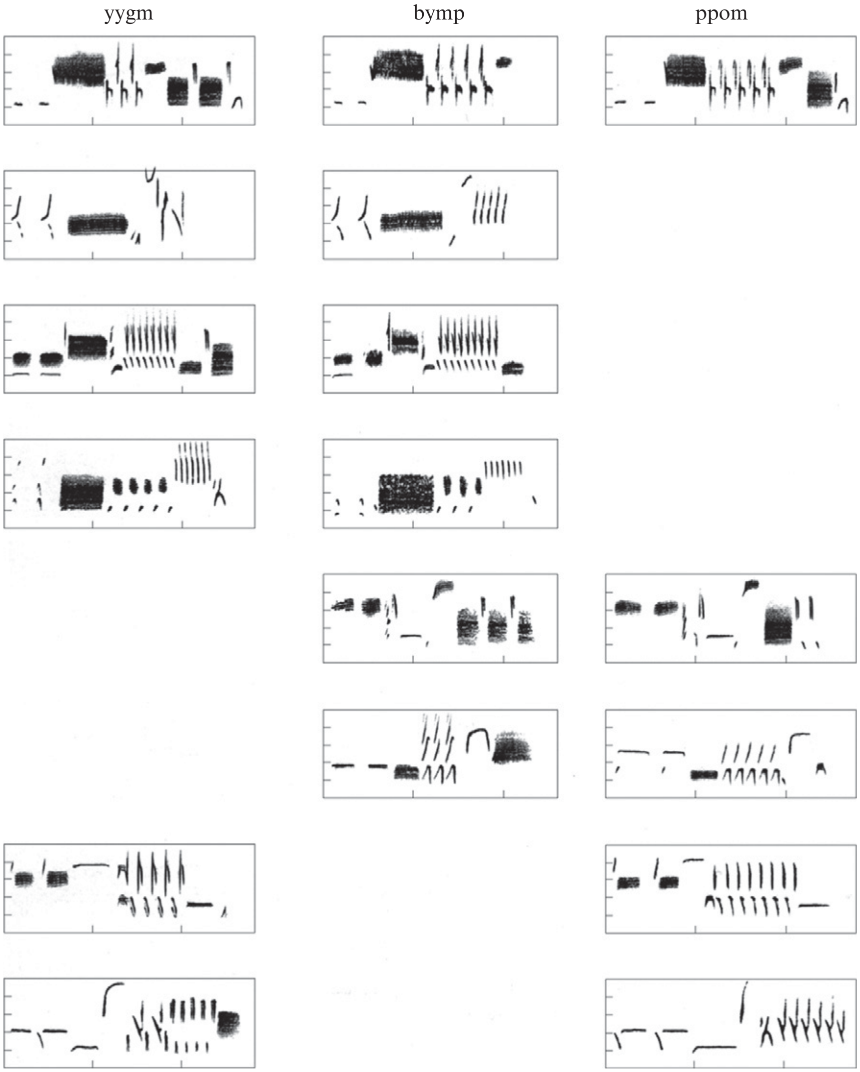


FIG. 7. Partial repertoires of three neighboring song sparrows: yygm, bymp, and ppom. Each row shows shared songs. To be considered shared, two songs had to match at least half of their component phrases. In borderline cases, we put more weight on the more invariant early portions of the song and less 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., see 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.

C. How Song Sparrows Use Their Songs

1. *Background: Song Matching*

Many studies have shown that birds will, at least under some circumstances, reply to a shared song with the same song type: ''song matching,'' or more precisely, *type matching* (reviews in Krebs *et al.*, 1981; McGregor, 1991; Smith, 1991). Most workers have viewed type matching as the bird's way of directing his response at the bird who has just sung. A puzzling finding has been that higher rates of type matching occur when the stimulus song is the bird's own song or a song of a stranger that is similar to one of the bird's own songs, than when it is a shared neighbor song (song sparrows, McArthur, 1986; Stoddard *et al.* 1992a; western meadowlarks, Falls 1985; great tits, Falls *et al.* 1982). Song sparrows, for example, match neighbor song only at about chance (~10%) level (Stoddard *et al.*, 1992a). We were able to shed some light on this finding in the course of a series of ''playback'' studies which I describe next.

In our playback experiments, we simulate a neighbor singing to the subject from near their mutual territory boundary (Fig. 8). In a key study in this series, we tested established song sparrow neighbors (mostly birds who had been neighbors for several years) in the mid to late breeding season. While these birds did not type match the broadcast neighbor song, they did consistently reply with some other song type they shared with that neighbor (Beecher *et al.*, 1996). That is, if the two birds shared three songs in their repertoires, say A, B, and C, but no others, then a bird would reply to a neighbor's A with B or C rather than A or any of his unshared songs. We have called this pattern of song selection *repertoire matching*. We hypothesized that repertoire matching represents a response that is directed but less intense than type matching. Song sparrows, like most songbirds, respond more aggressively to a song of a stranger than to one of an established neighbor, at least when the song comes from within that neighbor's territory (Stoddard, 1996; Stoddard *et al.*, 1990, 1991). Thus it seemed plausible that a song sparrow might respond aggressively to a brand new neighbor, type matching shared songs, but as the neighbor became better established (''Dear Enemies,'' see Section V.C.2) the antagonism would diminish and type matching be succeeded by repertoire matching.

To test this hypothesis, we compared a bird's response to the song of a neighbor that was new that breeding season. We did this twice during the breeding season: early, in April, and again a month and a half later (Beecher *et al.*, 2000a). Early in the breeding season, new neighbors will have only recently established their territorial boundary, which may still be in dispute, and territorial skirmishes will have occurred recently or may still be occurring. A new neighbor singing at the boundary early in the season

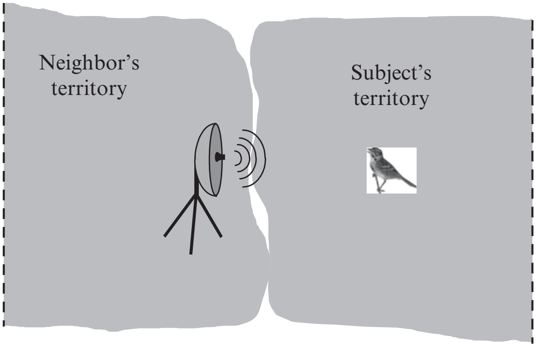


FIG. 8. The goal of our typical playback experiment is to measure the response of the subject to songs of his neighbor. We simulate a neighbor singing by broadcasting his song into the subject's territory from a directional speaker (fitted with a parabolic reflector). In all of the experiments discussed in this chapter, this ''playback'' speaker was placed just inside the neighbor's territory, near the two birds' mutual territory boundary. The neighbor generally does not hear the broadcast song (''playback'') unless he happens to be close, because the speaker is highly directional. However, he may hear the subject singing in response to the playback. For this reason, we either wait for the neighbor to be at the far back of his territory, or, better, one researcher lures the neighbor to that spot with low-level playback of stranger song. Territories are big enough that birds interacting at one boundary generally will not hear interactions at the opposite boundary, especially if they are each interacting with their own (simulated) intruder. If, despite our precautions, the real neighbor intrudes during the 3-min trial period, that trial is discarded and repeated on another day. We measure the intensity of the subject's response to the playback and also what songs, if any, he sings. The song playback can be noncontingent, that is, begun at some point when both birds are relatively quiet, or it can be contingent on the subject's response (''interactive playback''). In the latter case we might, for example, wait for the subject to sing a shared song, then present him with a type match (the neighbor's version of the same song type), a repertoire match (a different neighbor song they share), or a song they do not share (we observe the subject's song and compare it to his neighbor's song repertoire on our field computer). Measures of response strength include closest approach to the playback speaker (generally the best measure), number of flights (these are generally short, as the subject flits about looking for the intruder), latency to respond, and number of threat displays (soft songs and wing waves). Number of (normal) songs is generally not correlated with other measures of response intensity, probably because highly aggressive birds generally stop singing or switch to soft song. Nevertheless, we are typically interested in which particular songs the subject sings in response to the playback.

thus represents a more serious challenge than a well-established neighbor singing at that same boundary and we predicted higher levels of type matching on the earlier occasion. As predicted, early in the season, birds usually replied to a shared neighbor song with a type match, whereas a month and a half later they usually replied with a repertoire match (in this experiment they never responded with unshared song either early or late). These results are consistent with the hypothesis that type matching is a more aggressive or escalated response than repertoire matching.

In two subsequent playback studies (Beecher and Campbell, 2005; Burt *et al.*, 2001), we made additional discoveries about how song sparrow neighbors use their shared and unshared songs when interacting. First, type matching is a threat, that is, a bird responds more aggressively when type-matched by a neighbor than he does when repertoire-matched by him. Second, a bird that has been type-matched will escalate by staying on type (rather than switching to a new type) and responding aggressively. Third, a song sparrow can de-escalate an interaction by replying to a type-matching neighbor with an unshared song: Birds depart the scene sooner if the simulated opponent sings an unshared song than if he sings a repertoire match. Fourth, a bird responds to neighbor song sooner if it is a shared song than if it is an unshared song, which suggests that shared song is a directed signal.

The results of our playback studies taken together suggest that song sparrow neighbors (1) communicate preferentially with songs they share, (2) threaten by type matching, (3) send directed but less threatening signals by repertoire matching, and (4) de-escalate maximally by replying with an unshared song (or by not singing and leaving the scene). Thus our results suggest that when neighbors share some song types and not others, they may use their shared songs to mediate their territorial and other interactions as described in the next section.

2. *Singing Rules in the Intrasexual Context*

For a territorial species such as the song sparrow, the benefit of interaction by singing (counter-singing) is that it can substitute for more costly forms of negotiating territory boundaries, such as fighting. For example, if two male song sparrows cannot resolve the issue at a distance with song, they approach one another, cease singing, and switch to visual displays and ‘‘soft song,’’ a low-volume, structurally very different type of vocalization (Searcy *et al.*, 2006), and then often to fighting.

In species with song repertoires (about three-quarters of all songbirds), the singer has a ‘‘choice’’ of which of his various song types to sing. How do they make these choices? As indicated in the previous section, we have used experimental ‘‘playback’’ studies in which we simulate a neighbor singing near the subject’s territorial boundary to develop a picture of the *singing rules* used by territorial male song sparrows which seem to play an important role in maintaining neighbor relations and territorial boundaries (Beecher and Campbell, 2005; Beecher *et al.*, 1996, 2000a; Burt *et al.*, 2001, 2002; Stoddard *et al.*, 1988, 1990, 1991, 1992a). The key is how the birds use their shared songs. As noted above, song sparrows in our population typically share some but not all of their songs (typically they share two to five of their eight to nine songs), and they use the subset of shared types in a graded communication system. Some experience with one another is required for the two birds to learn the subset (a bird will share different subsets of his repertoire with different neighbors), but presumably they acquire this knowledge over the course of counter-singing bouts. Our studies have established that song sparrows in our population communicate according to the following rules.

Consider two hypothetical neighbors with 10 songs each who share three songs—A, B, and C—but no others. Bird 1 can ‘‘address’’ bird 2 by singing one of their shared types A, B, or C (toward bird 2, since other neighbors may also share some of the types). Let us say bird 1 sings A. Bird 2 then can ‘‘acknowledge’’ the signal by replying with B or C (repertoire match), or escalate by replying with A (type match), or de-escalate by singing one of unshared types, or ignore by not singing at all. If bird 2 type matches bird 1 (sings A), bird 2 can escalate further by continuing to sing that song type, or he can de-escalate by switching to another shared song (repertoire matching), or de-escalate further by switching to an unshared type. Note that to type match requires no prior experience with your 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 they share and which they do not. These ‘‘singing rules’’ are summarized in Figs. 9 and 10.

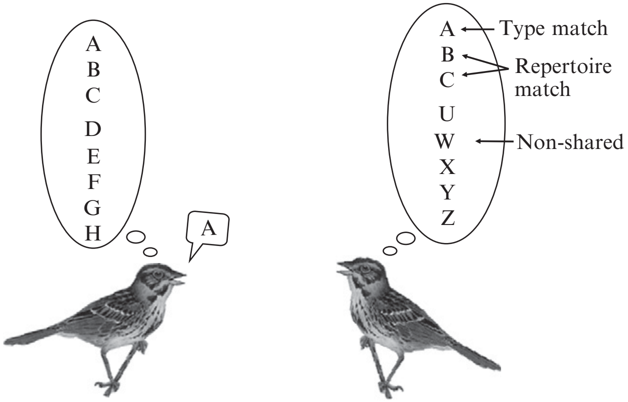


FIG. 9. A diagram of two neighbors who share three of their eight songs each (shared song types indicated by the same letter). The bird on the left begins the interaction by singing one of their shared songs, A. The bird on the right can reply by singing A (a type match, which escalates the interaction), B or C (repertoire matches, which are directed but less likely to escalate the interaction), or any one of his five remaining unshared songs (which generally de-escalates the interaction). Note that the diagram is not to scale: The birds would be fighting, not singing, if they were actually this close!

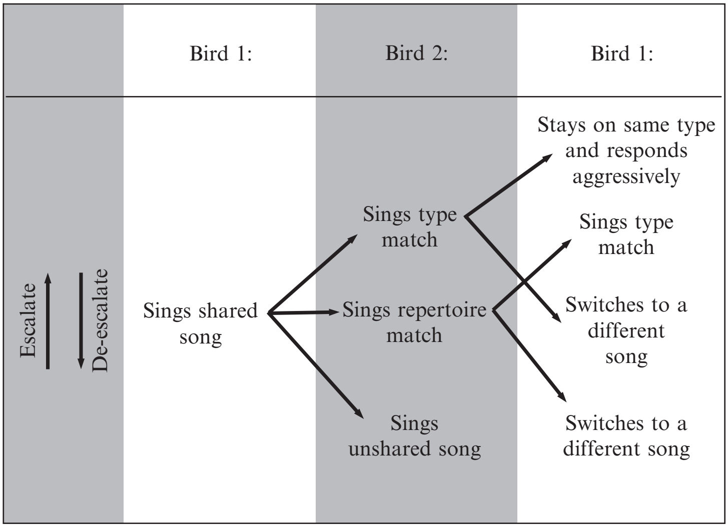


FIG. 10. Diagram of singing interactions between two neighbors who share some song types. Escalation is indicated by behaviors higher in the diagram, and de-escalation by behaviors lower in the diagram. In this figure, the interaction begins when bird 1 sings a shared song type. Bird 2 can then type match bird 1 (escalate), repertoire match (a directed but neutral signal), or sing an unshared song (de-escalate). If bird 1 is type matched, he may respond to the escalation by staying on the same type and responding aggressively (a further escalation) or de-escalate by switching to another song type and not responding strongly. Aggressive response refers to searching for, threatening, or attacking the singer.

A similar pattern of singing has been observed in the banded wren (Molles and Vehrencamp, 2001), another territorial bird with neighbor song sharing. The hypothesis that having shared songs facilitates communication between territorial neighbors is one hypothesis for the function of a song-learning program that leads to song sharing with neighbors. If the system of long-distance communication described here is beneficial in resolving most disputes with minimal cost, then we should see birds with shared songs faring better than those without shared songs. In Section V of this chapter, I will consider this and several other hypotheses about the benefits of song sharing.

3. *Intersexual Context*

As is the case for many songbirds, male song sparrows sing at a higher rate when they are unmated (unpublished data), and song clearly has a strong mate attraction role. Its role in close social interactions is more difficult to determine, and songbird researchers have generally resorted to using the copulation solicitation display as a preference assay (Searcy, 1992a). Searcy pioneered this technique with song sparrows, and showed that females preferred (gave more copulation solicitation displays) to playback of larger repertoires versus smaller repertoires (8 songs preferred over 4, 16 preferred over 8, Searcy, 1984). Searcy also found, however, that females showed no preference for larger repertoires in the field, when mate choice was measured by pairing date (Searcy, 1984).

We have examined the role of song sharing in mate choice (O'Loghlen and Beecher, 1997, 1999). We tested responses of female song sparrows to songs of their mates and neighbors, as well as to songs that were similar to or different from the songs of their mates. Females gave more copulation solicitation displays to songs recorded from their mates, fewer to songs of neighbor males, and fewest to songs of "stranger" males (males several territories removed). Among the stranger songs, however, females responded more strongly to songs that were most similar structurally to types in their mates' repertoires (matching songs). One interesting implication of the observed female preferences for neighbor over stranger song, and for matching stranger over non-matching stranger song, is that any male with songs structurally similar to mate songs or even to non-mate but local songs, might be at an advantage in sexual interactions with females in local neighborhoods. However, when we examined birds in our field population, we found no evidence that females preferred as extra-pair partners males who had local-shared songs (Hill *et al.*, manuscript in preparation). Approximately 25% of song sparrow chicks in the sample were due to extra-pair matings and the genetic father of the extra-pair chicks was always a neighbor of the female and her social mate, but extra-pair paternity was unrelated to repertoire size, the extent to which the extra-pair mates shared songs with neighbors, or the extent to which the extra-pair mates shared songs with the female's social mate. These results are reminiscent of Searcy's with eastern song sparrows, where laboratory preference tests suggested the importance of repertoire size but a field study failed to confirm this preference.

D. Function of Song Sharing and Song Repertoires

Several studies on the correlates of song sharing and song repertoires have suggested that these traits may be advantageous for male song sparrows. In a longitudinal study of 45 song sparrows followed from their first year on territory, we found that the number of songs a bird shared with his neighborhood group in his first breeding season predicted his lifetime territory tenure (range 1–8, mean = 2.82 years) but his repertoire size did not (Beecher *et al.*, 2000b). We also found that song sharing increased with repertoire size up to but not beyond 8–9 song types, which are the most common repertoire sizes in the population (range in our sample, 5–13). This partial confound of song sharing and repertoire size may account for an earlier finding of territory tenure–repertoire size correlation in song sparrows (Hiebert *et al.*, 1989), but see below. In another western population, this one in California, Wilson *et al.* (2000) found a positive correlation between the probability of a male song sparrow surviving and remaining on his territory from one year to the next and the number of songs the bird shared with adjacent neighbors. It has also been shown in this California population that song sparrows are less aggressive toward neighbors with whom they share songs (Wilson and Vehrencamp, 2001). In further studies of the Mandarte Island (B.C.) song sparrow population studied by Hiebert *et al* (1989), Reid *et al* (2004) found that first-year males with larger repertoires were not more likely to acquire a territory, to acquire a larger territory, or to settle sooner. They were, however, more likely to mate, and their mates were more likely to begin laying earlier. Song sharing was not measured in this study, and because of the partial correlation of song sharing with repertoire size, we cannot disentangle these effects. One possible interpretation of the data on western song sparrows is that song sharing plays a key role in male–male competition while repertoire size plays a key role in mate choice. Later in this chapter, I discuss similar studies that have been carried out with eastern song sparrow populations and other species.

E. Song Learning

1. *Field Studies: Methods and Approach*

In hopes of identifying the key social variables in song learning for our study species, we began our investigations in the field (Beecher *et al.*, 1994b; Nordby *et al.*, 1999). We chose as our study population a sedentary (nonmigratory) population of song sparrows in an undeveloped 534-acre park bordering Puget Sound in Seattle, Washington. We reasoned that if we color-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. Post-dispersal learning is the typical pattern in songbirds (see review in Beecher *et al.*, 1997). In our population, birds we have banded in the nest and subsequently recaptured within the population post-dispersal (typically having dispersed some distance from the nest) sing song types of their post-dispersal area rather than 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 in the years 1986–1990 (Beecher *et al.*, 1994b), we carried out a full-scale study of a cohort of 41 birds who hatched in 1992 and survived to song crystallization the following spring (Nordby *et al.*, 1999). We considered as possible song tutors all older birds in the study population who were on territory in the subject's hatching year. We identified the older bird with the most similar rendition of the type (complete with idiosyncratic features not seen in other renditions of the type) as the young bird's ''probable tutor'' for that type. This judgment is rarely problematic, because song sparrow songs are complex and similar songs stand out on the background of the nearly 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 neighbors share songs—they would both receive credit as the tutor for that song. We compared several different criteria, varying in strictness, for identifying a bird as a song tutor and happily they led to essentially the same conclusions, with the exception, of course, of the number of tutors identified (see discussion in Nordby *et al.*, 1999). Although in recent years we have developed automatic, computerized methods for analyzing song similarity, these methods are faster but not as accurate as the judgments of human observers. Hence in our analysis of song learning, we have relied on the judgments of multiple experienced human observers. These judgments have been informed by our extensive field observations of singing in this species, by the results of our field playback studies (Beecher *et al.*, 1996, 2000a; Burt *et al.*, 2001, 2002; Stoddard *et al.*, 1988, 1990, 1991, 1992a), and by our laboratory perceptual experiments (Beecher *et al.*, 1994a; Horning *et al.*, 1993; Stoddard *et al.*, 1992b). These issues are discussed in detail in Beecher (1996).

2. *Rules of Song Learning Inferred from Field Studies*

The results from our field studies are summarized below as ''rules of song learning.'' The bulk of these results come from Nordby *et al.* (1999), except those as indicated from Nordby *et al.* (2001, 2007) and Beecher *et al.* (1994b).

Rule 1: Copy songs of conspecific singers. Song sparrows copy almost nothing but song sparrow song in the field, despite the occasional copy of a song or song element of a Bewick's wren (personal observation) or white-crowned sparrow (Baptista, 1988). They will readily copy swamp sparrow song in the lab (Marler and Peters, 1988a), so it would appear their failure to do so in the field (except for on the odd occasion) implies a mechanism for selecting conspecific models.

Rule 2: Complete song learning by first spring. As established in field studies below, song sparrows can memorize new songs at least into their first autumn (until they are 6 months old) and we suspect that they may be able to do so into their first spring. In the field, they at least continue to modify their repertoire (drop songs, rearrange elements in songs) into their first spring. But they do not appear to change their song repertoires after their first breeding season (Nordby *et al.*, 2001).

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 made us realize that we could trace song learning in the field. 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. These field results differ from the comparable laboratory findings of Marler and Peters (1987, 1988a) using tape tutors. In the laboratory setting, song sparrows copy song *elements* quite precisely, but they frequently combine elements from different songs to form what we will call ‘‘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.

Rule 4: Learn the songs of multiple birds. It typically takes three to five song tutors to account for the young bird's entire repertoire of eight or nine song types. In Nordby *et al.* (1999), only 1 of the 41 subjects appeared to be a song ‘‘clone’’ of a single older bird.

Rule 5: Learn from your neighbors. Invariably, a bird's song tutors 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. One typical case is illustrated in Fig. 11. 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 and/or because other young birds moved into this area. The young bird appears to commence song learning shortly after he has dispersed from his natal area. Because adult males (potential song tutors) in our population typically will remain on their territories from one year to the next unless they die in the interim, it is essentially impossible for us to determine from field data *when* the young bird learns his songs. We originally thought that most or all of song memorization occurs in the traditional lab-determined sensitive period, roughly the second and third months of life (Marler and Peters, 1987), but this was only a plausible guess and our lab studies have cast doubt on that assumption (see below).

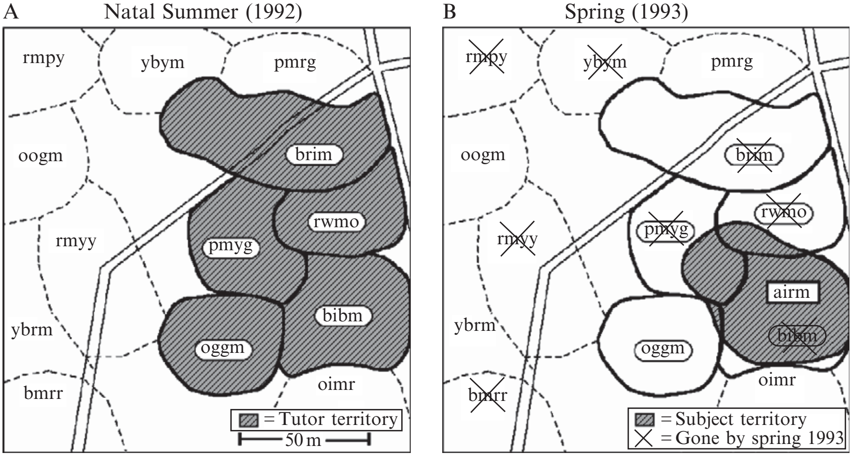


FIG. 11. (A) Territories of airm's tutors in his natal summer (1992). Adult birds (potential tutors) are shown by their color bands (four-letter codes) and their territories by dotted lines. The identified tutors of airm and their territories are shown by the dark hatching. (B) Territory of airm the 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; 4 out of airm's 5 tutors did not survive the winter. (This is an unusually high mortality rate: overwinter survival is typically 60–70%.) Note that airm established his territory in an area overlapping the former territories of 3 out of the 4 deceased tutors and next to his one surviving tutor (oggm). The young bird shared songs with the surviving tutor, and with other young birds who moved into that area as they had similarly learned songs of the area.

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 and/or spring. This would be the pattern hypothesized as typical by Nelson and Marler (Nelson, 1992; Nelson and 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 phases, and found that they do indeed retain songs that are more similar to those of their spring-time territorial neighbors, while dropping some songs that are less similar (Nordby *et al.*, 2007).

Rule 7: 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 to 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 *et al.*, 1994b). There are several possible reasons that shared song types might be particularly salient, including these: (1) they are heard more than unshared song types; (2) ''the same song'' is being sung by several birds; (3) they are heard more often in counter-singing interactions than are unshared songs. The last possibility is considered further below.

One interpretation of the function of the 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., share these songs with one neighbor only). But these specialized songs would be good only until the tutor dies or moves, whereas a shared song is good until all the birds having it in the neighborhood die or move, and probably even longer because other young birds moving into the area also preferentially learn shared types.

Rule 8: Individualize your song repertoire. The rules so far can be interpreted to fit the overall rule: Learn songs that you will share with your neighbors in your first breeding season. We have recently discovered, 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). One example is shown in Fig. 12. We interpret this as the bird ''individualizing'' his song. 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 his cake and eat it too: to have songs that are both shared with his neighbors yet unique to him. Even should this interpretation prove correct, however, we have no hypothesis for why the bird individualizes some of his songs but not others.

3. *Seminatural Lab Studies of Song Learning*

The next step after our field studies was ''semi-natural'' 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, for

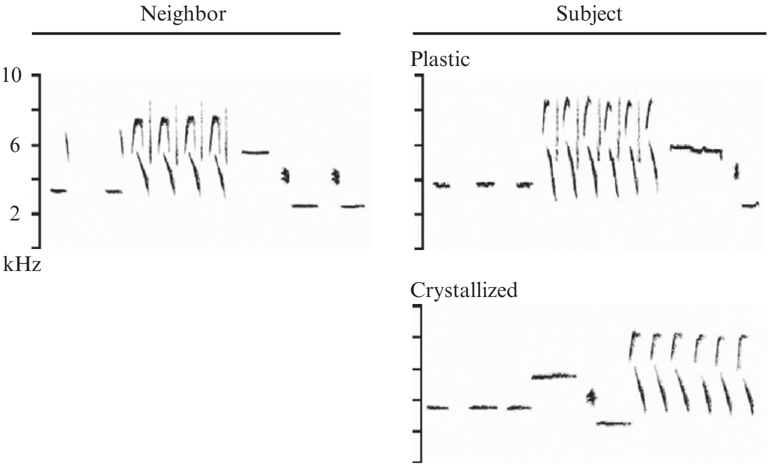


Fig. 12. An example of a song "individualized" by a young bird. Plastic version (top right) and crystallized version (bottom right) of a song type that bird GEMO shared with his neighbor and probable tutor (top left). In the young bird's plastic song (recorded in December and January), he has simplified the initial notes by dropping the upper part, but the rest of the song is a good imitation except for the wobbly pitch. Note that some of the differences between the prototype song of the adult and the plastic song of the young bird (top row) are within the normal range of variation on a type (e.g., three initial notes instead of two, one final note complex instead of two). Two small changes in the final, crystallized version, however, make the young bird's song look fairly different from the adult's song: GEMO has simplified the trill (left out one of the three notes in the repeated element) and has transposed the end segment to the middle of the song. It is likely that the two birds would nevertheless treat these songs as the same type (i.e., would type match or repertoire match as appropriate).

example, could move the young subjects nearer to or farther from particular tutors. We carried out two such studies (Nordby *et al.*, 2000, 2001). In both of them, we used aviaries on the roof of our laboratory building to simulate natural field conditions. Four adult males who had been neighbors in the field, and who shared some of their songs, were stationed on "territories" at the four corners of the roof. The "territories" were small aviaries containing a potted tree and numerous additional perches. The males did in fact become quite territorial about these "territories" and counter-sang with one another like song sparrows in the field. In both experiments, young birds were moved from territory to territory, as we believed they moved in the field (Arcese, 1987, 1989); we have recently begun radio-tracking young song sparrows to get more direct information on their behavior in this phase.

In our first experiment (Nordby *et al.*, 2000), we hand-raised eight young song sparrows and then put them through two phases of song learning. In Phase 1 (roughly June and July), they were moved from one tutor to another every few days, so that they got to see and hear each of the four tutors up close (one-quarter of the time) and hear each of them at a distance as well (three-quarters of the time). In Phase 2 (autumn and then again in the spring), the young subjects were split into one of two experimental conditions. For half of the subjects (''stationary'' group), a bird, when he was on the roof, was always next to a particular one of the four tutors. For the other half of the subjects (''rotator'' group), a bird, when he was on the roof, spent equal time next to each of the four tutors. Because the subjects themselves sing in this phase (unlike in the early phase), we had just four of them out at a time, with one each next to one of the four tutors. While one group of subjects was on the roof, the other group was in acoustic isolation.

All subjects learned from multiple tutors, usually from three or all four. The pattern of learning between the two experimental groups was quite different however. Subjects who were next to just one of the tutors in the late phase preferentially retained songs of that tutor for their final repertoire (''proximity'' effect). In contrast, the subjects who continued to rotate between tutors in the late phase, all learned the most from one particular tutor of the four. That tutor was not the most popular tutor overall for the four ''stationary'' subjects, so the proximity effect trumped the tutor effect (whatever that tutor effect may have been). We cannot specify, of course, the key variable for the proximity effect: Did birds learn most from the tutor they were stationed next to because they were next to him, or because they could see him (the other tutors were 13–17 m away and could not be seen), or because they interacted with him more in some way, or for some other reason altogether?

Our second experiment with live tutors (Nordby *et al.*, 2001) examined the question of late song learning. We used the same basic layout on the roof, again with four adult tutors who shared some songs with one another, each stationed in his aviary ''territory'' in one corner of the roof; note that these were different tutors from the previous experiment. We again rotated the young birds among these tutors in the early phase (June and July). The major manipulation occurred in Phase 2 (fall and spring), which took up after the birds had had ~2 months off (August and September, birds in isolation): We replaced two of the original tutors with two new tutors. Thus, there were six tutors from whom the young birds could learn songs: two were ''permanent'' (present in both phases), two were ''early-only'' (Phase 1 only), and two were ''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. We expected the subjects to learn the most from the permanent tutors and least from the late tutors, though we also thought that the subjects might prune their repertoires as

Marler and Nelson propose, retaining early memorized songs that were most similar to the songs of the late-only tutors. For the late phase, the 12 subjects were divided into three groups (“cohorts”); while one cohort was on the roof with the tutors, the other two cohorts were in acoustic isolation. When a subject was on the roof, he was always next to the same tutor (like the “stationary” subjects of the previous experiment).

The results of this experiment surprised us, and differed in several important ways from the results of the first experiment. Of the six tutors, one of the late-only tutors was the most effective tutor, with over half the songs learned by the 12 subjects traced to him. Virtually no songs of the two early only tutors were retained. The effectiveness of the late-only tutor occurred despite his late start (September 29), which is well past the end of classical critical period, and despite his never being close and visible to three-quarters of the subjects. Thus in this experiment, the tutor effect (whatever it may have been) trumped the proximity effect.

This second seminatural experiment confirmed the results of our first one in showing that late experience (from autumn on) was critical in determining a bird’s repertoire. However much of the late learning in the second experiment was not mere selections of earlier-memorized songs but in fact *de novo* learning of new songs. We have not pursued this question of how long *de novo* song learning is possible in song sparrows, and in particular, whether it can still occur in the spring, because we feel this question distracts from more interesting questions about song learning. But clearly the “late” (post-summer) phase is a crucial time for song learning in song sparrows, and our subsequent experiments have typically been designed with the major experimental manipulation occurring in the late phase.

This second study made two additional points. First, it showed that neither proximity nor visual contact was necessary for song learning. Second, it suggested that auditory interaction may be the critical variable in song learning. Although the experiment had not been set up to measure singing interactions, the song tutors were recorded for 1 h per day, and we observed that our supertutor—who accounted for ~50% of all songs learned—was extremely interactive with other tutors, and perhaps with the young birds as well (our recordings were inadequate on the latter point). Although he also sang more than the other tutors, we had not found a song rate (“dosage”) effect on learning in the previous experiment, and so we speculated that the key factor may have been that he sang interactively: He was much more likely to reply (sing shortly after) another tutor’s song than were any of the other tutors. These conclusions—the first strong, the second admittedly speculative—were crucial to the design of our next experiments and to the development of our “virtual tutor” system.

4. *Analytic Live Tutor Studies*

Our next experiment with live tutors (Beecher *et al.*, 2007) was less ‘‘natural’’ than our roof aviary experiments but we hoped that its stronger controls and experimental manipulations would permit stronger inferences than were possible from the roof experiments. We compared two types of song tutoring: that resulting from direct interaction with the song tutor, and that resulting from social eavesdropping, that is, overhearing the singing interactions of other birds. Again the major experimental manipulation occurred in Phase 2 of this experiment. Subjects were exposed to the songs of four tutors during the early ‘‘memorization’’ phase (Phase 1) of song learning and to just two of them again in the later ‘‘action-based’’ learning phase (Phase 2). As noted above, our field studies and our roof aviary experiments both indicated that birds are more likely to retain songs for their adult repertoire that they heard in their natal summer if they are exposed to them again the following spring. Thus, we assumed that birds would learn more from the two tutors present during both phases than from the two tutors present only in the early phase. As in the previous experiments, our experimental manipulation was carried out in Phase 2. Of the two tutors returning in Phase 2, one became a subject’s *interactive tutor,* while the other became the subject’s *overheard tutor*, that is, was overheard interacting with another, yoked subject. This yoked design is illustrated in Fig. 13. That is, on day 1, subject 1 interacted with tutor BO, while subject 2 overheard their singing. On day 2, subject 2 interacted with tutor PP, while subject 1 overheard their singing. Similarly, on day 1, subject 3 interacted with tutor PP, while subject 4 overheard them, while on day 2, subject 4 interacted with tutor BO, while subject 3 overheard them. Subjects 1–4 were isolated for the next 2 days while subject pairs 5 and 6 and 7 and 8 went through this same sequence.

We found that subjects learned (retained) more songs from their overheard tutor than from their interactive tutor (about twice as many on average). We ascertained that the subject learned songs of the overheard tutor, not of the overheard yoked subject, because the repertoire of a subject was no more similar to that of the yoked subject he overheard than it was to that of the non-yoked subjects he never heard. Although many interpretations of this result are possible, we consider just two. First, it may be that birds learn more from eavesdropping on singing interactions (Social Eavesdropping Hypothesis, Section III) than participating in them themselves (Direct Interaction Hypothesis). Second, and this hypothesis seems likely to be complementary to the previous hypothesis, the overheard interactions may have been less threatening. The close, intense nature of the interactive tutor vis-à-vis the subject may have been

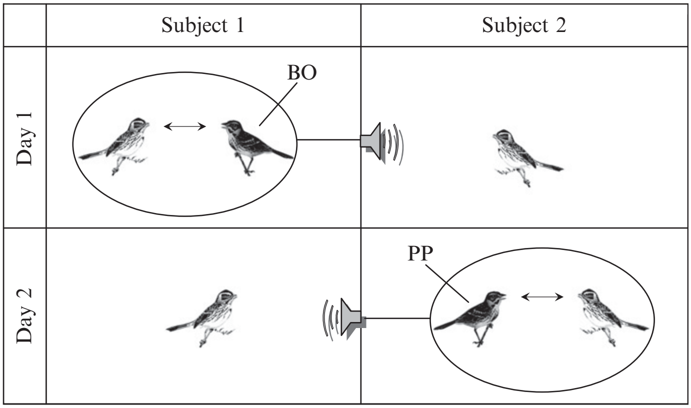


FIG. 13. Schematic representation of the yoked subject design (Beecher *et al.*, 2007). In Phase 2, a subject was exposed to one tutor live, the interactive tutor, on day 1, and overheard a similar tutor–subject pair on day 2. For one-half of the subjects, subject and interactive tutor were separated by a black cloth screen (not shown). Two birds, BO and PP, were used as tutors in this experiment. On days 3 and 4 (not shown), the young bird was returned to his home cage in a closed chamber. *Note:* The schematic representation does not show that the subject and interactive tutor were in their own separate cages within a larger sound-insulated chamber.

intimidating, thus diverting his attention to the overheard, ‘‘more distant’’ songs. Of the overheard pair, the subject learned the songs of the tutor, the older and presumably more dominant member of the yoked pair, rather than of the young bird (who, at least in the beginning, was singing obviously immature, plastic songs). However, while the results of this experiment provide stronger support for the Social Eavesdropping hypothesis than the Direct Interaction hypothesis, it is far from a ‘‘strong inference’’ contrast of the two hypotheses. In the next section, we discuss our development of a methodology that will permit such tests.

5. *Virtual Tutor Studies*

At the conclusion of our second seminatural (roof aviary) experiment (Nordby *et al.*, 2001), we made the following proposal:

> We suggest that in future studies it may be profitable to try and simulate live tutors and key aspects of the natural social situation using tape tutors. The experiment could be set up so that the ‘‘tutors’’ interacted with one another from separate ‘‘territories’’ and, ideally, with the tutees during the plastic song phase as well (antiphonal singing, song matching, etc.). This simulation would capture some features of the natural conditions, including spatial separation of singing adult males, clear definition of song types via shared song types, and interactive singing . . .. We suggest that . . . how the tape tutor

> "uses" its songs (e.g., to reply to, type match or overlap the tutee; to respond to some but not others of the tutee's songs; to interact with the other tutors) will outweigh how often particular songs are played. (p. 844, Nordby *et al.*, 2001).

In short, we envisioned a rapprochement of the tape tutor and live tutor paradigms, using recorded song in a sophisticated way to simulate live singing birds that could interact both with one another and with the subject as well. Digitized songs, computer programs, and powerful computers have made this possible, and we have dubbed the computer-simulated song tutors we have developed "virtual tutors." The virtual tutor method permits us to maintain the experimental rigor of the tape tutor paradigm, while capturing at least some of the key features of natural singing, especially interactive singing, as well as the ability to interact with the subject (Beecher and Burt, 2004).

The virtual tutor software, designed by John Burt (www.syrinxpc.com), can be programmed to (1) sing solo, non-interactively, that is, "posting mode," similar to a tape tutor, or (2) sing interactively with the subject, or (3) sing interactively with another virtual tutor. In the interactive modes, it interacts as a live song sparrow would, using singing and song type selection rules that we have extracted from our field observations and playback studies (especially Beecher *et al.*, 1996, 2000a; Burt *et al.*, 2001, 2002), as discussed in Section IV.B.1 above. When interacting directly with the subject, the virtual tutor can identify what the subject is singing and reply appropriately. For example, if the subject sings a song that is similar to one of the virtual tutor's, the virtual tutor can respond with that same song type ("song matching," see below). The repertoire of each virtual tutor is based on that of a real bird and consists of 8–10 song types, with 8–10 variations on each type (Podos *et al.*, 1992; Stoddard *et al.*, 1988). When more than one virtual tutor is used in an experiment, each virtual tutor's songs are played from different loudspeakers in the subject's chamber. Virtual tutors are fixed to particular loudspeakers to reinforce the impression that the subject is positioned between two neighbors.

We realized that we might be able to capture—purely acoustically—the key features of normal singing interactions when the best tutor in our second roof aviary experiment taught songs to young birds who could hear him at a distance but not see him (Nordby *et al.*, 2000, 2001). And in the live tutor experiment just described (Beecher *et al.*, 2007), birds learned equally well from interactive tutors whether there was a blind between the young bird and the tutor or not (half the birds had the blind, half did not). Several other experiments with songbirds have also indicated that the tutor does not have to be seen to be effective (Adret, 2004; Bolhuis *et al.*, 1999).

Our first studies with the virtual tutor program were pilot studies to see how well it would work (Burt *et al.,* manuscript in preparation). In the first study (Burt *et al.*, unpublished), hand-raised birds were exposed to virtual tutors only; the virtual tutors were interactive among themselves but did not attempt to match the subjects. The young subjects developed songs like birds in the field: they copied whole songs, copied multiple tutors, and preferred tutor-shared songs. In a second study (Burt *et al.,* unpublished), we collected birds from the field in August when they were 3–4 months old (exact age unknown) and had presumably had ample song tutoring in the wild (details of course unknown). Lab tutoring with four virtual tutors began in late October, when the birds were at least 5 months old. The singing of the virtual tutors was interactive, both with one another and with the subject (though they did not attempt to match the song). All subjects developed normal repertoires, with about half of the songs drawn from the late virtual tutors. This is impressive considering that the subjects did not hear the virtual tutor songs until they were 5 months old, and not until after several months of song tutoring by real birds in the wild.

In another experiment (Burt *et al.*, 2007), we used a hybrid design: In the early phase (early summer), young birds were exposed to two pairs of interacting live tutors on alternate days. In the second phase (January through March), the subjects were isolated and exposed to digitized songs from two of these tutors (i.e., they were now "virtual tutors"), one tutor from each of the two original pairs. On alternate days, a subject heard songs from each of the two tutors; for each subject, one of the tutors was *interactive,* and the other was *noninteractive* (i.e., was just heard singing solo). The amount of song from each subject's interactive and noninteractive tutors was equated.

Subjects learned (or retained) more songs from the late interactive tutor than from the late noninteractive tutor. Interestingly, subjects also learned/retained more songs from the early singing partner of the late interactive tutor. This implies that the young bird remembered the singing interactions he heard the previous summer and selected his songs from those he overheard sung to his present interactive tutor 6 months earlier. Thus these results, like the results of the live tutor experiment (Beecher *et al.*, 2007) discussed in the previous section, also point to the importance of overheard singing interactions, though in this case the overheard interaction had occurred in the early phase rather than in late phase of learning. The results of these two experiments taken together suggest that social interaction may indeed be critical for song learning, but in both cases, it appears that the key social interaction was an overheard one.

We are presently carrying out a virtual tutor experiment in which subjects are exposed to two sets of virtual tutors (each tutor is given his own loudspeaker, and apparent territory direction). One pair of tutors is interactive, interacting in accordance with the "western song sparrow" rules described above, and the other set is noninteractive (they sing the same number of songs as the other pair, but they never interact). This study will provide a strong test of the Social Eavesdropping hypothesis, according to which the subjects should learn more songs from the interactive pair than from the noninteractive pair.

V. Discussion

A. Hypotheses on the Function of Song and Song Learning

In this chapter, I have focused on the song-learning program of one particular species, but as noted in Section I, perhaps the most impressive aspect of the song-learning programs of songbirds is the incredible interspecific diversity. One cannot discuss the function of a song-learning program without some hypothesis about what it is supposed to accomplish, and in this section, I describe some of the many hypotheses of song function in the literature.

Most functional hypotheses of song have focused on the adult song repertoire, and have not directly addressed the song-learning strategy by which the bird reaches that final repertoire. That is, these hypotheses about song function have to be extrapolated to hypotheses about the function of the underlying song-learning program. Moreover, most of these functional hypotheses have focused on either the intrasexual or the intersexual context and ignored the other (Beecher *et al.*, 1994b; Kroodsma and Byers, 1991). In some cases this narrow focus may be justified. For example, in sedge warblers, males sing incessantly until they have attracted a mate, and then stop singing altogether (Catchpole, 1976), indicating that the intersexual function of song predominates. But in most species, the evidences suggest that song functions in both intrasexual and intersexual contexts.

Most hypotheses of song function have had a narrow focus in a second respect, namely, in viewing song repertoires or song sharing to be the target of selection. For this reason, I will refer to these two classes of theories hereafter as the *Repertoire* and *Sharing hypotheses.* According to the *Repertoire hypothesis*, the song-learning program functions to give the bird a large song repertoire, while according to the *Sharing hypothesis*, it functions to give the bird songs he shares with his neighbors or group members. Although these two goals are not incompatible, song sharing does not require a large repertoire, and in some cases may favor smaller repertoires (see below).

1. The Repertoire Hypothesis

There is considerable empirical support for the hypothesis that repertoire size is under strong directional sexual selection in some songbirds (reviews in Catchpole and Slater, 1995; Gil and Gahr, 2002; Searcy and Andersson, 1986; Searcy and Yasukawa, 1996), and in some cases the evidence suggests that repertoire size is driven by female choice. The sedge warbler, just mentioned, provides one example. In laboratory studies, Catchpole and colleagues have shown that females give more copulation solicitation displays to large repertoires than to small repertoires (Catchpole *et al.*, 1984), and in field studies they have shown that females choose large-repertoire males before small-repertoire males (Buchanan and Catchpole, 1997). However in a recent study of this species, it was found that contrary to prediction, extra-pair males had smaller song repertoires (and smaller territories) than the female's social mate. Other studies have suggested that in the polygynous great reed warbler, large-repertoire males get more mates than do smaller-repertoire males (Catchpole, 1986) and more extra-pair matings as well (Hasselquist *et al.*, 1996). However, a recent study and reanalysis of the earlier data (Forstmeier and Leisler, 2004) have indicated that the harem size–repertoire size correlation disappears when corrections are made for territory quality and male age (repertoire size increases with age), suggesting that when there is enough competition for territories, older, larger-repertoire males get the better quality territories, and females choose mates on the basis of territory quality. Although song sharing also varies in this population, it has not been measured in these studies.

In comparative studies of four species of warblers, Catchpole found that repertoire sizes are larger in monogamous species (including the sedge warbler) than in polygynous species, which he explains as due to more intense female choice in the monogamous species; he argues that females choose territories in the polygynous species and males in the monogamous species (Catchpole, 1980). In contrast, in a comparative analysis of eight species of North American wrens, Kroodsma found the reverse correlation between mating system and repertoire size: Polygynous species had larger song repertoires than did monogamous species (Kroodsma, 1977). Kroodsma suggests, however, that male–male competition, rather than female choice, may be the factor driving increases in repertoire size (Kroodsma, 1988).

The generality and applicability of the Repertoire hypothesis is seriously limited, however, by the fact that the majority of songbird species have just one or a few songs. About 30% of species have single-song repertoires, and at least another 50% have very small repertoires (fewer than five or so song types), hardly the acoustical equivalent of the peacock's tail. Small repertoires can perhaps be explained as resulting from the high costs of large repertoires, with the costs generally hypothesized to relate to the demands on brain space made by repertoires and/or the effects of stress on the development of song repertoires (Garamszegi and Eens, 2004; Gil and Gahr, 2002; MacDonald *et al.*, 2006; Nowicki *et al.*, 1998; Pfaff *et al.*, 2007). This hypothesis is supported by the finding by Buchanan *et al.* (2004) that brain centers involved in song learning are selectively affected by developmental stress in zebra finches. This finding also raises the question, however, of whether large-repertoire species would be more affected by this cost than would small-repertoire species such as the zebra finch. Finally, phylogenetic studies suggest that song repertoires have been lost in some lines, for example, in emberizine sparrows and blackbirds (Irwin, 1988, 1990). In some of these single-song species, repertoires appear to be disfavored despite a female preference (measured by copulation solicitation display tests in the lab) for large (supernormal) song repertories (Searcy, 1992b). These questions, taken with the prevalence of small-repertoire (including one-song) species, suggests that we should consider alternative hypotheses that posit selection pressures on some aspect of song other than repertoire size.

2. *The Song-Sharing Hypothesis*

One advantage of plasticity is that a bird can copy the songs of group mates or territorial neighbors, and thus ‘‘share’’ songs with them. Most studies that have examined neighbors for song sharing in repertoire species, or song similarity in single-song species, have found greater similarity between neighbors than between non-neighbors (e.g., marsh wrens, Verner, 1975; bobolinks, Avery and Oring, 1977; indigo buntings, Payne, 1982; village indigobirds, Payne, 1985; tufted titmice, Schroeder and Wiley, 1983; great tits, McGregor and Krebs, 1982; corn buntings, McGregor and Thompson, 1988; field sparrows, Nelson, 1992; Smith’s longspur, Briskie, 1999; yellow warbler, Beebee, 2002; and see reviews in Catchpole and Slater, 1995; Handley and Nelson, 2005). There are other populations, however, where birds share no more with neighbors than with other birds in the population (e.g., chaffinches, Slater and Ince, 1982; western meadowlarks, Horn and Falls, 1988; Kentucky warblers, Tsipoura and Morton, 1988; Gambel’s white-crowned sparrows, Nelson, 1999; and of especial interest here, most eastern song sparrow populations, Hughes *et al.*, 1998). Some of these exceptions to the rule may be Type-II errors, that is, failures to detect a difference (neighbors songs are more similar than non-neighbors songs) that is actually present. This kind of error is possible given the very conservative sharing criteria used by most researchers. As noted earlier, 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 the totally different birds who are now their neighbors. This process would produce populations where neighbor song sharing might not pass the song-sharing threshold applied by our group or the Searcy–Nowicki group, for example, or indeed by most song researchers, but might be detectable by someone looking for these subtle similarities. An excellent example has been provided by Nelson (1992). Field sparrow males return to the breeding area with two or three songs; Nelson showed that they retained the one that most closely resembled the song of the most actively singing neighbor (although the song similarities might not have satisfied the usual song-sharing criteria). In any case, the degree of song similarity between neighbors will surely be greater in populations where birds learn their songs directly from their neighbors than in cases where they follow the more indirect Nelson–Marler selection process.

Song sharing is found in a variety of social contexts, not only in territorial neighbors (the most commonly studied context) but also in lekking species and in communal breeders (Brown and Farabaugh, 1997; Payne and Payne, 1997; Trainer, 1989). This ubiquity of song sharing has led some workers to suggest that song sharing may be the most general function of song learning; this idea has been stated most strongly by Brown and Farabaugh: ‘‘vocal learning has evolved to allow individuals to share vocalizations with a particular subset of conspecifics, such as territorial rivals or flock mates, rather than with any conspecific’’ (1997, p. 99).

Although the Sharing hypothesis might seem to have a better chance at broad generality than the Repertoire hypothesis given that song sharing among neighbors has been found in the majority of species that have been carefully examined, a problem for the Sharing hypothesis is the rival, more parsimonious hypothesis that birds learn songs that are more similar to those of their neighbors or group members simply because these are the birds they happen to encounter in the song-learning phase. If the cast of neighbors (or group members) remains reasonably stable after the song-learning phase, the young bird will wind up sharing songs with these neighbors (or group members). This more parsimonious hypothesis means one must identify additional design features or make additional predictions that distinguish between the hypothesis that song sharing is adaptive and the simpler hypothesis that is merely an incidental consequence of song learning in a stable neighborhood (or group) context. We return to this point below.

The first proposed Sharing hypothesis was the *Genetic Adaptation* hypothesis (Baker, 1975; Nottebohm, 1970). According to this hypothesis, 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 dialect 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 as herself. This theory requires (1) an adaptive correlation between geography and population genetic structure, (2) a predictive correlation between dialect and population genetic structure, and (3) female choice of mates who sing the local dialect; a parallel hypothesis could be developed concerning male–male competition, although no one has done so to date. There is little direct support for the Genetic Adaptation hypothesis. Two recent studies of white-crowned sparrows give conflicting results, with one group (MacDougall-Shackleton and MacDougall-Shackleton, 2001) finding a weak correlation of dialect and population genetic structure in California populations of *Zonotrichia leucophrys oriantha* and another group finding no such correlation in Oregon and Washington populations of *Z. l. pugetensis* (Soha *et al.*, 2004). Finally, there seems to be an underlying logical problem with the Genetic Adaptation hypothesis: Would not a female do better to base her choice on a signal that more directly reflects the local genome, rather than on a learned signal which can be (and often is) learned far from the natal area? Nevertheless, it is possible that a learned signal could be a better predictor of geographic origin than a signal with a direct genetic basis (e.g., Boehm and Zufall, 2006), and with the increasing sophistication of genetic methods, better data sets relating to this hypothesis may be on the way. The other attraction of this hypothesis is that a female preference for local songs might be favored both for the direct benefits—a local male might be more competitive and a better parent (see Badge hypothesis below)—and for the indirect benefits (locally adapted genome).

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 newcomers being confused with established birds and thereby receiving reduced aggression. Craig and Jenkins also argued that a song repertoire is a counter-adaptation to mimicry, that is, an established bird could maintain his individuality by singing more song types than the newcomer could mimic. The Mimicry hypothesis has received little support. It is inconsistent with the many experiments showing well-developed individual recognition in songbird species with song sharing (review in Stoddard, 1996). Moreover, direct tests have failed to support the hypothesis (e.g., McGregor and Krebs, 1984; Payne, 1983). In a playback experiment that tests this hypothesis about as directly as can be done, Wilson and Vehrencamp (2001) compared the aggressive response of song sparrows to (1) neighbor songs, (2) stranger songs that were highly similar to (i.e., ''mimicked'') neighbor songs, and (3) non-mimic stranger songs. The birds responded just as aggressively to mimic stranger songs as to non-mimic stranger songs, and more aggressively to either than to neighbor songs.

The *Badge* hypothesis has been formulated most explicitly by Rothstein and Fleisher (1987) and more informally in several other papers (Beecher *et al.*, 1997; Brown and Farabaugh, 1997; Wilson and Vehrencamp, 2001). According to this hypothesis, shared songs serve as a badge of familiarity in groups and among territorial neighbors. In the case of territorial neighbors, the Badge hypothesis is closely associated with the *Dear Enemy* hypothesis (Fisher, 1954; Getty, 1987; Jaeger, 1981; Temeles, 1994; Ydenberg *et al.*, 1988), which suggests that long-term neighbors should be preferred to new neighbors because new neighbors are inherently expansionist, whereas old neighbors generally respect territory boundaries once they have been established. Beletsky and Orians (1989) have shown that male red-winged blackbirds with familiar neighbors have greater breeding success than do males with unfamiliar neighbors. Neither preferring nor cooperating with familiar neighbors requires shared songs, of course, but shared songs are a reliable signal of familiarity or locality since they must be learned in the local neighborhood. Another variation on the Badge hypothesis has been offered recently by Lachlan *et al.* (2004).

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 and 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 signaling 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 (though if dispersal is not far, this distinction could be irrelevant).

3. *Are the Repertoire and Sharing Hypotheses Mutually Exclusive?*

A tendency among bird song researchers that has bedeviled the field has been to focus on one particular context (e.g., mate choice or male–male competition) or one particular song trait (e.g., song repertoires or song sharing) or one particular species. But multiple selection pressures may act on song and they may act on several different aspects of song. For example, in the case of western song sparrows, the results of the studies cited earlier might be taken to indicate—if some inconsistencies are ignored—that female choice selects for large song repertoires and male–male competition (in the context of territory acquisition and maintenance) selects for song sharing (Beecher *et al.*, 2000b; Reid *et al.*, 2004; Wilson *et al.*, 2000). While this interpretation is probably still too simplistic, it at least is a step up from the viewing selection as acting on *either* repertoire size *or* on song sharing.

The next step will be to consider other song traits that might be the target of selection. Song *performance* is one such candidate. Songs can be difficult or costly to sing, and the ability to perform songs well might be especially attractive or salient to receivers, possibly providing information as to the quality of the singer. An example that is likely relevant to song sparrows is the trade-off between trill rate and frequency bandwidth, first pointed out by Podos (1997): Songs with simultaneously fast trill rates and wide bandwidths are difficult to sing. Although I do not consider this variable further in this chapter, interest in performance as a important characteristic of a bird's song has increased in recent years (e.g., Ballentine *et al.*, 2004; Beebee, 2004; Byers, 2007; Cramer and Price, 2007; Forstmeier *et al.*, 2002) and seems likely to enter the fray as a serious hypothesis for explaining song evolution.

Finally, these different selection pressures may compete, pushing song traits in different, and sometimes opposite directions. That selection for song sharing and selection for large song repertoires are at least partially contrary is a simple logical consequence of the fact that a song-learning strategy cannot optimize both traits. Song learning designed to maximize the number of songs copied from a set of birds (e.g., present neighbors) cannot also maximize the percentage of songs shared with this or a similar set of birds (e.g., the future neighbors). The bird that learns just those songs shared by his tutor-neighbors will necessarily have both a smaller repertoire and a higher sharing index than will the bird who learns all of their songs.

If the function of the song-learning program is the acquisition of a repertoire of songs shared with certain key individuals, it is generally true that this goal can be met with a relatively small repertoire. Thus, the Sharing hypothesis could explain the prevalence of small repertoire species, while specifying a counter-force that might hold down repertoire size in species with intermediate-sized repertoires.

The Sharing hypothesis provides a novel perspective on the difference between birds that do not modify their repertoires after their first year (*aged-limited* or *closed-ended* learners) and birds that do (*open-ended* learners). If the function of the song-learning program is give the bird songs that are similar to those of his neighbors, then an open-ended learner could add and drop songs each year so as to increase song sharing with his new neighbors. Such a pattern has been observed in several species so far examined (Lemon *et al.*, 1994; Martens and Kessler, 2000; McGregor and Krebs, 1989; Rasmussen and Dabelsteen, 2002; Sorjonen, 1986; Trainer, 1989). A similar result has been found for birds that change their song in the beginning of their first or second breeding season (Briskie, 1999; O'Loghlen and Rothstein, 2002; Payne and Payne, 1997). Moreover, the optimal repertoire size should be smaller for open-ended learners than for comparable closed-ended learners, because open-ended learners have the opportunity to replace non-matching songs with matching songs. Contrariwise, a closed-ended learner does not have the ability to change his repertoire to increase sharing, but if he has more songs to begin with, he has a better chance of coming up with a suitable match. Supporting this prediction, open-ended learners that replace songs *so as to increase sharing* have been found to have smaller repertoires than comparable closed-ended learners (Griessmann and Naguib, 2002; Kipper *et al.*, 2004; Lemon *et al.*, 1994; McGregor and Krebs, 1989; Payne and Payne, 1997).

If the most general prediction of the Sharing hypothesis is that the song-learning program should equip the birds with songs that he shares with his neighbors, then what is the best song-learning strategy in populations where neighbors change within as well as between breeding seasons? Kroodsma (1996) has argued that for birds without long-term neighbors, there is no advantage to shared songs, and so the development of generalized species-typical songs will be favored. The sedge wren (*Cistothorus platensis*) provides a test 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 neighbors. 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 and Verner, 1978; Kroodsma *et al.*, 1999a). Consequently, each bird winds up with a repertoire of unique songs, and two neighbors in the field (who probably will not be neighbors for long) will share no song types. In contrast, the closely related but sedentary marsh wrens faithfully copy tutor songs in comparable experiments, and in the field they share songs with their neighbors (Kroodsma and Pickert, 1984a; Verner, 1975). Furthermore, tropical populations of sedge wrens are sedentary, in contrast to the seminomadic northern populations, and this tropical sedge wrens show the common pattern of song sharing with neighbors that is generally taken to imply song learning from neighbors (Kroodsma *et al.*, 1999b).

B. THE SONG SPARROW SONG-LEARNING PROGRAM: AN ADAPTIVE STRATEGY?

We have made good progress in characterizing the song-learning program of song sparrows in our study population, identifying eight "rules" that taken together might be considered an adaptive learning strategy (Section IV.D.2). These are: (1) Learn songs preferentially from conspecific singers. (2) Complete song learning in the first year. (3) Copy song types completely and precisely. (4) Learn the songs of multiple birds. (5) Learn from your neighbors. (6) Preferentially learn or retain song types of those tutors who survive into your first breeding season. (7) Preferentially learn tutor-shared songs. (8) Individualize (at least some of the songs in) your song repertoire.

Taken together, Rules 3–7 work to maximize the number of songs the young song sparrow will share with his neighbors, especially his near neighbors, in his first breeding season, while maintaining some individuality in his songs. They are consistent with the *Sharing hypothesis* that the underlying song-learning program has been shaped by the advantages of sharing songs with neighbors. They are also consistent with our finding of a positive correlation between song sharing and survival (Beecher *et al.*, 2000b).

However, we should be cautious about classifying Rules 3–7 as adaptations of the song-learning program. As Williams has admonished, "Adaptation is often recognized in purely fortuitous effects, and natural selection is invoked to resolve problems that do not exist" (p. 4, Williams, 1966). A skeptic could look at the evidence we have presented and argue that it is not necessary to call Rules 3–7 "adaptations." The skeptic could argue that all we have observed could be explained with just Rules 1 and 2 (learn preferentially from conspecific singers in your first year of life) and two additional basic assumptions, that the bird is most likely to learn songs he hears most often (*dosage effect*), and songs of birds he is near most often (*proximity effect*). Dosage could explain why a bird is more likely to learn tutor-shared songs than tutor-unique songs (the former are heard more often since two or more tutors sing them) and why the bird is more likely to learn (retain) songs of tutors who survive the winter (their songs are heard more often), while proximity could explain learning from multiple neighbors (the bird is closer to neighbors than to non-neighbors, and he has multiple neighbors). This dosage-proximity hypothesis must be seriously considered in light of the finding, mentioned above, that eastern song sparrows typically do not share songs with their neighbors.

Song sparrows are one of numerous songbird species that show marked population differences in singing (e.g., Canady *et al.*, 1984; Ewert and Kroodsma, 1994; Kroodsma and Verner, 1978; Kroodsma *et al.*, 1999a,b).

While song sparrow populations show only modest variation in repertoire size (Peters *et al.*, 2000), they show marked variation in song sharing among neighbors. In all western populations carefully surveyed so far (in Washington, California, and British Columbia), birds typically share two to four songs with a given immediate neighbor, but none with birds just a few territories removed (Beecher *et al.*, 1994b; Cassidy, 1993; Hill *et al.*, 1999; Nielsen and Vehrencamp, 1995; Reeves and Beecher, manuscript in preparation; Wilson *et al.*, 2000). In eastern populations (Pennsylvania, Maine, Ontario), on the other hand, birds rarely share songs with neighbors, and share no more with neighbors than with non-neighbors (Borror, 1965; Harris and Lemon, 1972, 1974; Hughes *et al.*, 1998; Kramer and Lemon, 1983; but see Foote and Barber, 2007).

This difference between western and eastern populations of song sparrows with respect to song sharing brings the question of song-learning adaptations to a head. Perhaps the reason song sparrows in western populations wind up with neighbor-shared songs while song sparrows in eastern populations do not, is simply because western birds have a stable set of tutor-neighbors, while eastern birds do not. That is, song sharing may be simply an incidental consequence of neighborhood stability in sedentary western populations, rather than a selected feature of an adaptive song-learning strategy. Song sparrows in eastern migratory populations may be equipped with the same song-learning program as their western counterparts, and fail to develop shared songs because neighbor turnover within and between breeding seasons is too great. In this respect, eastern song sparrows may resemble the northern sedge wrens described in the previous section.

Hughes *et al.*, however, propose a different hypothesis, suggesting that the difference in song sharing between the two populations is the result of a difference in the underlying song-learning programs: ‘‘Washington and Pennsylvania song sparrows differ in how they learn song, in that Washington birds copy whole songs, while Pennsylvania birds appear to copy and recombine song segments, as has been found in laboratory studies of song learning.... Thus both song learning and the function of song repertoires differ between populations of song sparrows’’ (Hughes *et al.*, 1998, p. 437).

The Hughes *et al.* argument assumes that song sharing is adaptive in western populations but not in eastern populations. This assumption is plausible, given that, as Kroodsma has suggested for northern sedge wrens, song sharing with neighbors may be neither possible nor beneficial in populations where a bird does not have long-term neighbors. Recently, Hughes and colleagues have gathered evidence suggesting that song sharing is indeed not advantageous in their Pennsylvania population: Unlike in our Washington population, they found no correlation between song sharing and survival (Hughes *et al.*, 2007). It is not clear, however, whether such an advantage could be detected given the low level of sharing that exists in this population.

C. The Comparative Method and the "Common Garden" Experiment

Population contrasts of the sort just described provide our best route to addressing functional questions. Specifically, they provide us a way to determine precisely which aspects of a song-learning program can be considered *adaptations.* Identifying adaptive differences in the song traits of two closely related species, or populations of a single species, is not sufficient to conclude that there are differences in the song-learning programs of the two, because the adaptive difference may simply be a facultative response to the differing environments.

To illustrate this problem, consider two hypothetical closely related species or populations of a single species (for simplicity, I say "populations" throughout). Suppose that a male of population A typically has 10 or so songs in his song repertoire, whereas a male of population B typically has 100 or so. Suppose further that we have determined that this difference reflects an *adaptive fit* to their different environments: 10 is optimal for the typical environment of A and 100 is optimal for the typical environment of B. Perhaps this relates to differing population densities experienced by A and B which leads to more intense competition among males in population B. While this may be an adaptive difference, it does not necessarily reflect differences in the underlying song-learning programs of population A and B, because the same song-learning program could underlie both phenotypes, with repertoire size being a facultative response to the differing environments. For example, in the denser population, birds might interact with more adult song tutors during the song-learning phase and thus learn more songs than birds in the less dense population. Alternatively, the two population could have evolved differing song-learning programs, each of which leads to the mean optimum repertoire size for the population-typical population density. For example, the window for song learning (the sensitive period) might remain open longer for birds in population B than those in population A, so that birds of population B learn more songs. Or more brain space for songs may be allotted for population B than for population A, so B males can learn more songs than A males (e.g., Canady *et al.*, 1984).

Thus in the first case above, the song repertoire difference is a *proximate* effect of the environmental difference—birds of population B learn more songs because there are more song tutors—and no difference in the underlying song-learning program is needed to explain the difference in repertoire size. In the second case above, the song repertoire difference is an *ultimate* effect of the environmental difference, in that the difference in song characteristics can be traced to differences in the underlying song-learning programs. In either case, the fit of repertoire size to the local population density is adaptive, but it is only in the second case that we can say that the difference is due to an adaptation, an underlying difference in the song-learning programs of the two populations.

A method that we could use to determine whether song differences between two species (or two populations of one species) reflect differences in the underlying song-learning programs, rather than facultative or plastic responses of a particular song-learning program to environmental differences, is the *common-environment* or *reciprocal-environment* experiment (Kawecki and Ebert, 2004). In this method, individuals of the different species or populations are exposed to a common environment (or ‘‘common garden’’) or to both environments (where the interesting case is the ‘‘reciprocal’’ transplantation, that is, individuals of species A exposed to the environment typical of species B, and vice versa).

Although this design has not been used as much as it should be in the study of song learning, there are several notable examples, including Kroodsma and Canady’s (1985) comparison of eastern and western populations of marsh wrens with respect to repertoire size, Marler and Peters’ (1988a,b) 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 *et al.*, 1995, 1996a,b). In each of these cases, clear differences between the two populations or species exposed to a common tutoring regime have been demonstrated, indicating differences in the genetic-developmental program underlying song learning. For example, when measured in the field, the song repertoires of western marsh wrens are about twice as large as those of eastern marsh wrens, and this difference persists when young birds from both populations are raised in the laboratory under a common tutoring regime. Kroodsma suggests that the difference between eastern and western marsh wrens may be traced to the greater population densities of western marsh wrens, selecting for larger repertoire sizes due to increased male–male competition; this scenario is similar to the hypothetical example I gave above.

In summary, a common garden comparison of eastern and western song sparrows provides a clear way to address the question of whether selection has acted on western song sparrows so as to increase the probability of song sharing with neighbors. Eastern and western birds exposed to a common tutoring regime might show the differences suggested by Hughes *et al.* in the quote above, or perhaps some other sort of difference. If no difference between eastern and western birds was found, that would be evidence for the simple dosage-proximity hypothesis we have suggested as an alternative. Finally, we would argue that comparative studies of this sort are precisely what the field needs to analyze possible adaptations of the developmental mechanisms of song learning.

D. Phylogenetic Approaches to the Evolution of Song

The other major approach to identifying adaptations is the comparative or phylogenetic method in which we superimpose song traits on a known phylogeny (Harvey and Purvis, 1991; and for a recent example, Raine *et al.*, 2006). Several recent studies have correlated song traits with ecological and evolutionary variables that might be expected to affect song. These studies, though few in number, converge on the general conclusion that song traits are extremely labile in evolution. In two pioneering studies, Irwin (1988, 1990) found that variation in song repertoire size is not explained by directional sexual selection in either emberizine sparrows or New World blackbirds. In both groups, the phylogeny suggests that the common ancestor of the group was a repertoire species, thus indicating selection for smaller repertoires in several of the extant species. Price and Lanyon (2004) looked for a correlation between the intensity of sexual selection and song complexity in the oropendolas and caciques. They detected effects of sexual selection, but found that different aspects of song have been affected in different lineages. Handley and Nelson (2005) examined 65 populations in the family Fringillidae. They found that song sharing or "dialects" have evolved rapidly in response to local conditions, being responsive to whether the species is migratory or sedentary and to breeding latitude (higher song sharing for sedentary species and species breeding at low latitudes). Local song sharing was randomly distributed on the phylogeny. Repertoire size and song sharing were uncorrelated, consistent with my suggestion in Section V.A. that these two traits may be responsive to different selective forces.

These phylogenetic studies suggest that song provides multiple potential targets for selection and thus different evolutionary patterns may have emerged in different lineages (Price and Lanyon, 2004). If this is generally true, it points to the importance of framing comparative analyses of song within a phylogenetic framework. A phylogenetic analysis might reveal, as these recent analyses suggest, that song-learning programs have evolved along different trajectories in different lineages. For example, perhaps the same selection pressure, say female choice, has favored different responses in different lineages, for example, large song repertoires in one, high-performance song in another, lifetime song learning in another, and song mimicry in a fourth. The major roadblock to this phylogenetic approach is the paucity of comparative data on the details of song learning, compared to more easily measured song traits such as repertoire size.

What accounts for the interspecific diversity of song and song learning in the songbirds? Although pure functional hypotheses provide a start, future hypotheses will almost surely need to be placed in a phylogenetic context. As we have argued elsewhere (Beecher and Brenowitz, 2005), the most difficult problem for functional hypotheses is presented by different songbird lineages responding to similar selection pressures with different modifications of the song-learning program. For example, the song-learning programs of sedge warblers and marsh wrens may have been driven by sexual selection to the same end of developing a large song repertoire. But the differences in the song-learning programs of these two species—marsh wrens require external song models (Kroodsma and Pickert, 1980, 1984a), whereas sedge warblers do not (Leitner *et al.*, 2002)—might best be explained not in terms of different selection pressures but in terms of different ancestries.

E. Conclusions and Future Directions

In our research program, we switch between questions about proximate mechanisms (including developmental mechanisms) and questions about ultimate causes (function). We attempt to integrate these approaches because we believe they will prove to be synergistic. Proximate and ultimate questions, while logically independent, are intimately intertwined in any realistic evolutionary scenario. If particular mechanisms (including developmental ones) are the target of selection, then we cannot understand function without understanding mechanism, and vice versa.

The goal of identifying the *adaptations* underlying song learning—in the strong sense of Williams (1966)—can be approached in a third way besides the common garden and comparative-phylogenetic approaches I have suggested. If a putative adaptation can be characterized well enough, it may be more readily explained as serving a particular specific function than as an incidental consequence of some more basic set of adaptations. To illustrate this point, we believe we will be able to distinguish—albeit only partially, and indirectly—between the sharing and dosage-proximity hypotheses with results from virtual tutor experiments. For example, we can have two virtual tutors sing one of their pairs of shared songs (call them A1 and A2) interactively, and another pair of their shared songs (B1 and B2) noninteractively. If the young bird hears these four songs, and other unshared songs of the virtual tutors, equally often, and yet shows a learning preference for A, we have eliminated dosage as the important variable. While a test of a proximate hypothesis does not directly address a functional hypothesis, some proximate mechanisms are more consistent with a particular functional hypothesis than others. This (hypothetical) finding would be evidence that a bird's learning is shaped more by how his tutor-neighbors use their shared songs when communicating, than by how often he hears the particular songs, and would be more consistent with the hypothesis that the shared song-learning preference is an adaptation ''for'' sharing songs with neighbors. In short, we feel that our experiments can provide insight not only into questions concerning the proximate mechanisms of song learning but as well into functional questions concerning possible adaptations of song-learning programs.

As a final point, I would argue that future studies of social factors in song learning should focus on the three hypotheses outlined earlier in the chapter (see Fig. 2). Our lab studies so far have provided stronger support for the Social Eavesdropping hypothesis than for the Direct Interaction hypothesis, but this research is clearly just in the beginning stages. In addition to laboratory approaches, however, these hypotheses can be evaluated directly in the field (Fig. 3). The field approach is free of the problems of ecological validity that have beset lab studies of song learning (Beecher, 1996) and has become feasible with recent advances in radio telemetry permitting the radio-tagging of small passerines (e.g., Norris and Stutchbury, 2001). Locating young songbirds in the field can be a challenge: They are often quite inconspicuous, and indeed in certain phases of their development, they may strive to be so. It is now possible to locate and track radio-tagged young songbirds and to observe in the field the extent to which they directly interact with adults and/or eavesdrop on the adults' solo or interactive singing. We are pursuing this direction at present (Templeton *et al.*, unpublished) and we recommend it to the field at large.

VI. Summary

In this chapter, I examine song learning in the oscine passerines (songbirds) from several angles, with special attention to our study species, the song sparrow. I focus on social factors and suggest that previous research on song-learning points to three different hypotheses about their role. According to the *simple eavesdropping hypothesis,* the young bird need only overhear an adult bird singing to learn song (this situation is mimicked by the classic ''tape tutor'' design). According to the *direct interaction hypothesis,* the young bird needs to interact with the song tutor to learn songs (this situation is mimicked by the early ''live tutor'' designs). And according to

the *social eavesdropping hypothesis,* the young bird learns best by eavesdropping on singing interactions between adult tutors. Thus in this last case, social interaction is critical, but the young bird need not directly participate in it. These hypotheses are not mutually exclusive, but each makes some distinctive predictions, and we have argued that the hypotheses can be rigorously tested using our ''virtual tutor'' design, in which a computer simulates interacting song tutors and/or interacts directly (sings) with the young bird. We are presently carrying out these studies.

I describe our field and laboratory studies of song sparrows. I give particular attention to how the birds use their songs in the normal territorial context because these interactions may be crucial to song learning, especially if the social eavesdropping hypothesis proves to be true. Song sparrows in our population typically share songs with their neighbors, and song sharing is a good predictor of a bird's lifetime territory tenure. I summarize our field studies of song learning in terms of ''rules'' of song learning (e.g., learn the songs of several, neighboring males, preferentially retain songs these tutor-neighbors share). Our roof-top ''semi-natural'' studies confirm many of these findings, and make several additional points. First, learning proceeds throughout the first year, right up to the bird's first breeding season, and memorization of new songs can occur at least into the bird's first fall, a much longer learning period than was previously thought. Second, counter-singing between song tutors seems especially important. Third, a song tutor does not have to be seen to be effective. Our subsequent, more analytic lab studies suggest that eavesdropping on singing interactions may indeed be critical in song learning, and they have stimulated us to turn to the ''virtual tutor'' method to analyze social interaction factors more rigorously.

I discuss the two most popular classes of hypotheses of song function—that song repertoire size or song sharing is the target of selection—and consider their relation to song-learning programs. Finally, I return to the question of which aspects of the song sparrow song-learning program—in particular those that seem to lead to song sharing among neighbors—can be considered evolved adaptations. The question is whether song sparrows learn shared songs because their song-learning program, in some way, leads them in that direction (the ''sharing hypothesis'') or as an incidental consequence of their movements. Doubts about the sharing hypothesis arise from a notable population difference in song: neighbors in western song sparrows share songs, whereas neighbors in eastern song sparrows typically do not. This population difference raises both doubts about the adaptation hypothesis and an opportunity to test it. I suggest that a ''common garden'' experiment, in which young birds from both populations are raised under a common tutoring regime, would directly address this question. Finally, I suggest that our studies on the proximate mechanisms of song learning may also help us address this question, because when we have adequately characterized the mechanisms of song learning, we may find that they are most consistent with one particular set of hypothesized song-learning adaptations.

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