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CHAPTER THREE

Aggressive Signaling in Song Sparrows and Other Songbirds

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1. INTRODUCTION

As is typical of passerine birds, male song sparrows (*Melospiza melodia*) hold individual territories, which they defend against other males of the same species. Defense is accomplished using a variety of displays backed up when necessary by physical aggression. Territory defense is thus the context for most of the aggressive signaling that is performed in this and other songbird

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species. Aggressive signaling in the context of territory defense is subject to the same issues regarding signal reliability that apply to aggressive signaling, in general (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005), but also brings into play additional considerations having to do with the maintenance of stable relationships with territorial neighbors. Territorial signaling has been intensively studied in song sparrows, perhaps more intensively than in any other animal. A review of the song sparrow signaling system thus has much to tell about how territorial signaling functions.

Aggressive signals usually communicate information either about the fighting ability of the signaler or about its aggressive intentions (Searcy & Beecher, 2009). For both types of information, selection may favor exaggeration (Maynard Smith, 1974, 1979), and some mechanism for maintaining signal reliability must be in place to make the signaling system evolutionarily stable and thus persistent. In the case of signals of fighting ability, the mechanism maintaining reliability is often a causal relationship between physical attributes of the signaler and properties of its signals. Displays whose reliability is maintained in this way are termed "index signals" (Maynard Smith & Harper, 1995, 2003). Index signals often communicate information on body size, as with call frequency in frogs and toads (Martin, 1971, 1972), and formant frequency in red deer (Reby & McComb, 2003). In songbirds, body size is not as important to fighting ability as it is in many taxa and index signals are more likely to communicate aspects of motor performance (Byers, Hebets, & Podos, 2010) rather than body size.

Signals of aggressive intent are sometimes simple to produce and therefore unconstrained by physical abilities (Rek & Osiejuk, 2010). The reliability of such signals is thought to be maintained by signaling costs other than production costs (Zahavi, 1975, 1977), in particular, by receiver-dependent costs (Guilford & Dawkins, 1995; Vehrencamp, 2000). Signals whose reliability is maintained by receiver-dependent costs rather than by intrinsic costs, and whose meaning is therefore arbitrary with respect to their physical design, are termed "conventional signals" (Guilford & Dawkins, 1995). Game theory models of aggressive communication have shown that receiver retaliation against highly aggressive signals can select against bluffing and hence can maintain reliability (Enquist, 1985). Most such models consider symmetrical signaling encounters (Szalai & Számadó, 2009; Számadó, 2000), but the basic mechanism also works when there is an asymmetry between competitors (Gardner & Morris, 1989), as is the case when one competitor is a territory owner and the other is an intruder. Such models often produce equilibria at which some individuals reliably signal their true aggressive intentions while other individuals exaggerate theirs (Gardner & Morris, 1989; Szalai & Számadó, 2009; Számadó, 2000).

Owners are expected to have an advantage over nonowners in territorial systems, either because of a "resource holding power" asymmetry (owners on average have higher fighting ability than nonowners), a value asymmetry (the value of a territory is higher for an owner), or an arbitrary asymmetry (an asymmetry correlated with neither fighting ability nor value) (Krebs, 1982; Maynard Smith & Parker, 1976). Empirically, territory owners often do have an advantage, in the sense that they win more contests against nonowners than expected by chance, sometimes far more than expected (e.g., Baugh & Forester, 1994; Rhodes & Quinn, 1998; Sandell & Smith, 1991; Yasukawa & Bick, 1983). Thus, territorial signals can in part be viewed as simply proclaiming the signaler's status as a territory owner. A proclamation of ownership should be more effective if the signals are individually recognizable, so that receivers can identify the signaler as a long-term resident rather than a recent substitute. Such a system is particularly effective if nonowners as well as owners tend to be long-term residents of a neighborhood, so that they too become familiar with the signals of territory owners. Long-term residency by nonterritorial "floater" males is common in songbirds (Arcese, 1987; Penteriani, Ferrer, & Delgado, 2011; Smith, 1978).

In territorial systems with long-term residents, neighboring territory owners are expected to adopt "dear-enemy" relationships with each other (Fisher, 1954). Such relationships are evidenced by reduced aggressiveness of established neighbors toward each other's signals (Weeden & Falls, 1959). Neighbors may go beyond merely tolerating one another and actually aid each other in defending territories against nonowners. Mutual aid of this type is predicted by game theory models that incorporate either reciprocity in aid-giving (Getty, 1987) or a cost to renegotiating boundaries with a newcomer (Getty, 1987; Krebs, 1982; Mesterton-Gibbons & Sherratt, 2009). Given the characteristics of their territorial and signaling systems, song sparrows provide an excellent model for examining dear-enemy relations and cooperative defense.

Territorial signaling in song sparrows has been studied at various points in the species' range, providing an opportunity to examine geographic variation in this signaling system. Song sparrow song, the primary aggressive signal of this species, varies geographically, as is true for the songs of many songbirds (Marler, 1952; Marler & Tamura, 1962; Podos & Warren, 2007) and for both acoustic and visual signals of other animals as well (Endler, 1995; Wilcynski & Ryan, 1999). What is unusual about territorial signaling in song sparrows is that geographic variation also has been found in functional aspects of the signaling system, such as in the meaning of particular signaling behaviors, their effects on receivers, and their relationship to fitness. A major goal of this chapter is to make sense of the pattern of geographic variation in functional aspects of song sparrow signaling.

Before turning to the aggressive signaling system of song sparrows, we provide some background on the natural history of this species.

2. NATURAL HISTORY OF SONG SPARROWS

2.1. Territoriality and Mating System

In all populations of song sparrows, adult males defend individual territories during the breeding season, but in other respects seasonal patterns of territoriality vary greatly between populations. In the northernmost parts of their range, virtually all individuals migrate south in the fall (Davis & Arcese, 1999), so the territorial system perforce breaks up for part of the year. At the other extreme, song sparrows are completely nonmigratory in some Pacific Coast populations and males defend their territories year round (Arcese, 1989). Intermediate patterns exist, in which some individuals migrate and others are resident all year (Nice, 1937, 1943) or in which no one migrates but territories are nevertheless abandoned during the winter (Wingfield & Monk, 1992). Year-round territoriality should lend itself to the establishment of long-term relationships between neighbors, but even in migratory populations males often defend the same territories in successive years (Hughes & Hyman, 2011; Nice, 1937), so that long-term relationships are still possible. Memory of neighbors and their songs has been shown to last from one breeding season to the next in another migratory songbird (Godard, 1991).

Song sparrows are primarily socially monogamous, with a single female associating with a single male on his territory. In a semi-migratory population in Ohio, Nice (1937) found that pairs break up at the end of the summer and rarely get back together in the following year, but longer lasting associations may be more common in nonmigratory populations. As is common in temperate passerines (Griffith, Owens, & Thuman, 2002), the genetic mating system is not as strictly monogamous as is the social mating system: in each of two molecular genetic studies of song sparrows, about a quarter of all young were sired outside the monogamous pair bond (Hill, Akçay, Campbell, & Beecher, 2011; O'Connor et al., 2006).

2.2. Song

Song is strongly associated with territory defense in song sparrows. Nice (1943), in her classic studies of song sparrows in Ohio, found that male song production peaks in late winter, when territories are established, and decreases to zero in winter, when territories are abandoned (Nice, 1943). Female song sparrows overall sing far less than do males (Arcese, Stoddard, & Hiebert, 1988; Nice, 1943), just as they are in general less active in territory defense. Nevertheless, when females do sing, it is usually in the context of territory defense, especially defense against other females (Arcese et al., 1988).

Male song (Fig. 3.1) usually begins with a syllable that is repeated to form a trill, followed by a "note complex," that is a group of unrepeated notes (Mulligan, 1963; Podos, Peters, Rudnicky, Marler, & Nowicki, 1992). Typical songs have three to five such phrases. Within this general format, a great deal of variation exists at a number of levels. A key feature of the song sparrow song system is that each male sings multiple versions of the species' song (Fig. 3.2). Individual repertoire sizes vary geographically (Peters, Searcy, Beecher, & Nowicki, 2000), but most males in all populations sing between five and 13 song types. Another level of song variation occurs within song types (Podos et al., 1992; Saunders, 1924). Here males change minor features of a song type from performance to performance and are especially likely to add, subtract, or substitute notes at the end of songs.

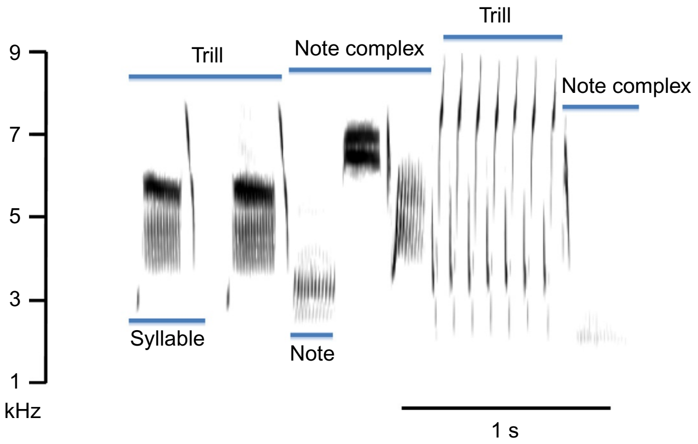

Figure 3.1 A spectrogram of a typical song sparrow song, showing the division into phrases of two types, trills and note complexes. Also shown is a syllable (the unit of repetition in a trill) and a note (a continuous sound).

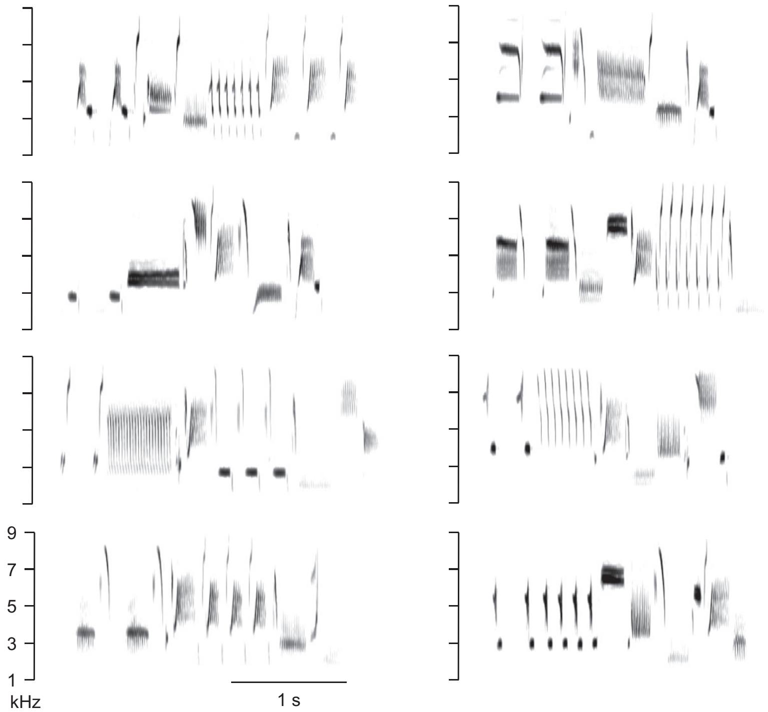

Figure 3.2 The song-type repertoire of one male song sparrow recorded in northwestern Pennsylvania. This male has eight song types, which is the most common repertoire size in many song sparrow populations. Other individuals in the same population have repertoires as small as five song types and as large as 13. As is typical, the song types within this repertoire are extremely different in their details.

Although the differences between such "song variants" are often subtle, playback experiments show that song sparrows attend and respond to this level of variation (Searcy, Podos, Peters, & Nowicki, 1995; Stoddard, Beecher, & Willis, 1988). Songs also vary geographically, as is shown by the differential response of song sparrows to songs from their own locales versus songs from other areas (Harris & Lemon, 1974; Searcy, Nowicki, & Hughes, 1997, Searcy, Nowicki, Hughes, & Peters, 2002).

The fact that male song sparrows each sing multiple song types and multiple variants of those types complicates the task of recognizing individuals by song alone. Nevertheless, evidence shows that song sparrows are capable of such recognition. In a Go/NoGo operant conditioning paradigm, captive male song sparrows learned to discriminate 32 pairs of song types and were adding new pairs as quickly at the end of the experiment as at the beginning

(Stoddard, Beecher, Loesche, & Campbell, 1992). The 64 songs learned in this study are equivalent to roughly eight individual repertoires. Song sparrows typically have two to six immediate neighbors, so males apparently have the capacity to remember the songs of all their immediate neighbors plus some nonadjacent ones. Female song sparrows show preferential courtship response in captivity to songs of their own mates over songs of neighbors and preferential response to neighbor song over stranger song (O'Loghlen & Beecher, 1997, 1999). Territorial males also show evidence of individual recognition by song (Stoddard, Beecher, Horning, & Campbell, 1991). Song sparrows show no ability to associate together the different song types of one individual by common "voice" characteristics (Beecher, Campbell, & Burt, 1994), so recognition of individuals by song seemingly must involve learning and remembering each song type an individual sings.

2.3. Song Learning

Song sparrows reared in acoustic isolation from other individuals develop abnormal songs (Kroodsma, 1977; Marler & Sherman, 1985), whereas young males exposed either to recorded songs or to live tutors produce songs that closely resemble species-typical adult song (Beecher, 1996; Marler & Peters, 1987). Song sparrows thus show vocal learning. Song learning appears to be universal in songbirds, but strategies for learning vary substantially among songbird species (Beecher & Brenowitz, 2005). Because a song repertoire adapted for territory defense is presumably one of the chief outcomes of song development, the song-learning strategy of song sparrows has implications for our understanding of how song functions in territory defense in this species.

Patterns by which songs are culturally transmitted have been worked out for a nonmigratory population of song sparrows in Seattle through a combination of field and laboratory studies (Beecher, 2008; Nordby, Campbell, & Beecher, 2001). Males in this population learn songs from potential neighbors after natal dispersal, that is, after they have left the territories where they were born and have moved to the areas where they will establish their own territories (Beecher, Campbell, & Stoddard, 1994; Nordby, Campbell, & Beecher, 1999). During the period in which they learn their songs, young males visit as many as 30–40 territories, gradually reducing their home ranges from their natal summer to the subsequent spring, when their home ranges become normal-sized territories (Templeton, Reed, Campbell, & Beecher, 2012). Young males learn songs from multiple males encountered during this period (Beecher, Campbell, & Stoddard, 1994; Nordby, Campbell, Burt, & Beecher, 2000; Nordby et al., 1999, 2001), preferring to learn songs that are sung by more than one potential neighbor (Beecher, Campbell, & Stoddard, 1994; Nordby et al., 1999, 2001). A young male is especially likely to retain in his repertoire songs that are sung by neighbors that survive into his first breeding season, often biasing his final repertoire toward one particular neighbor's repertoire (Nordby et al., 1999). Once the repertoire of song types is crystallized at 1 year of age, it does not change thereafter (Nordby, Campbell, & Beecher, 2002).

The song-learning rules emphasized above seem designed to maximize the sharing of songs between neighbors, implying that song sharing is selectively advantageous. Beecher (2008), however, cautions that sharing patterns may result solely from a simpler, underlying rule by which young males learn the songs they hear most often and most clearly. Another caveat is that there may be geographical variation in song-learning strategies within song sparrows, specifically with respect to whether young males copy whole songs or parts of song. Studies of western song sparrows have found mostly whole-song copying (Beecher, Campbell, & Stoddard, 1994; Nordby et al., 1999), whereas studies of eastern song sparrows have found mostly copying of parts of song, such as syllables and phrases (Marler & Peters, 1987, 1988). Differences in the methods of these studies, however, complicate this comparison: western birds have been studied mainly in the field with natural tutoring, whereas eastern birds have been studied exclusively in the laboratory with tape tutoring. Studies of western birds using captive subjects exposed to live tutors (Nordby et al., 2000, 2001) produced less whole-song learning than field studies (Nordby et al., 1999), but a western study with interactive tape tutoring (Beecher, Burt, O'Loghlen, Templeton, & Campbell, 2007) produced whole-song learning very nearly as high as in the field studies. A strong test for geographic variation in song learning would require an experiment in which western and eastern song sparrows were raised and tutored under identical conditions (Beecher, 2008); as no such study has been done, conclusions about geographic differences in learning must remain tentative.

3. FUNCTIONS OF SONG

Song has two principal functions in most songbirds: in territory defense against other males and in attracting and courting females (Searcy & Andersson, 1986). By "function" we mean an effect of song that is selectively advantageous to the singer and which therefore can explain the evolutionary maintenance of the behavior. A variety of evidence supports a male–female function of song in song sparrows (Nowicki, Searcy, & Peters, 2002; O'Loghlen & Beecher, 1997; Reid et al., 2004; Searcy & Marler, 1981), but as our focus here is on aggressive signaling, we will not review this evidence.

Observational evidence provides indirect support for a territory defense function of song in song sparrows. Territory establishment coincides with the onset of adult singing behavior in young song sparrows (Nice, 1937). Singing rates vary seasonally and the highest rates coincide with the most intense period of territory defense early in the breeding season (Nice, 1937, 1943). Various changes in singing behavior occur during natural or simulated intrusions on territories (Kramer & Lemon, 1983; Kramer, Lemon, & Morris, 1985), suggesting that these changes might help in repulsing an intrusion.

More direct evidence that song functions in territory defense can only be provided by experiments. Across songbirds, in general, two experimental designs have been used to test the territory defense function. In muting experiments, territorial males are deprived of the ability to produce song by means of a minor surgical intervention. Results of muting experiments are in accord with the hypothesized function in that birds deprived of the ability to sing suffer increased intrusions and/or loss of all or part of their territories (McDonald, 1989; Peek, 1972; Smith, 1976, 1979). No muting studies have been done with song sparrows. In speaker occupation experiments, an owner is removed from his territory and replaced by loudspeakers, which in the experimental treatment play conspecific songs and in the control treatment play either nothing or some neutral sound such as white noise. In speaker occupation experiments with other songbirds, territories defended by song playback have consistently been reoccupied more slowly than control territories (Falls, 1988; Göransson et al., 1974; Krebs, 1977; Yasukawa, 1981), indicating that song repels other males and thus aids in territory defense.

One speaker occupation experiment has been performed with song sparrows. Nowicki, Searcy, and Hughes (1998) chose pairs of song sparrow territories from within single old fields and randomly assigned one territory in each pair to the experimental treatment and one to the control. The owners of both territories were removed, as simultaneously as possible. Once males had been removed, playback started on the experimental territory, using songs from the removed owner, and rotating periodically between two speakers. No songs were played from control territories. The two territories were then monitored for the next 14–18 h of daylight. Male song sparrows, either neighboring territory owners or nonterritorial males, invaded eight of 11 control territories sometime during the observation periods; by contrast, only three of 11 experimental territories were invaded. In eight of eight pairs of territories where an invasion occurred, the control territory was invaded before the experimental territory. The results are thus consistent with song being effective in territory defense in song sparrows.

4. AGONISTIC DISPLAYS OF SONG SPARROWS

4.1. Background

Song sparrows give a variety of displays in aggressive contexts; these are best termed “agonistic” rather than “aggressive” displays (Scott & Fredericson, 1951) in order not to prejudge whether they are actually threatening. Most but not all of these displays involve song. We will focus on those aspects of display that have been well studied in song sparrows: (1) song rate, (2) switching frequency, (3) soft song and wing waves, and (4) song-type matching and repertoire matching. We will neglect agonistic displays that have been studied in other songbirds but not in song sparrows, such as frequency matching (Foote, Fitzsimmons, Mennill, & Ratcliffe, 2008; Morton & Young, 1986) and song overlapping (Naguib & Mennill, 2010; Searcy & Beecher, 2009).

A small number of experimental designs have been used repeatedly to investigate territorial displays in songbirds. In “simulated territorial intrusion,” playback of conspecific song, sometimes paired with a taxidermic mount, is used to simulate an intrusion of a conspecific male onto a subject’s territory. The display under investigation is measured in this aggressive context and compared to the same display given in a control context to determine whether the display is exaggerated or otherwise modulated during aggression. In “territorial playback,” the display of interest is played via a loudspeaker to subjects on their territories. Response to the display is compared to response to a control stimulus as a test of how receivers respond to the display. Aggressive response is assessed via behaviors such as close approach to the speaker and number of flights given by the subject. In “mount attack experiments,” a subject is first provoked to give aggressive display and is then given the opportunity to attack a taxidermic mount of a conspecific. Subsequent analysis determines whether the display or displays of interest predict which subjects attack the mount and which do not attack.

4.2. Song Rate

Perhaps the most basic attribute of singing behavior is song rate. Singing has some energy cost in songbirds, though more through decreased energy intake (Reid, 1987) than through increased metabolic expenditure (Oberweger & Goller, 2001). An energy cost makes song rate a candidate for a reliable signal of energy balance. In a number of songbirds, song rates have been shown to increase in individuals that are experimentally provided with extra food (Alatalo, Glynn, & Lundberg, 1990; Davies & Lundberg, 1984; Searcy, 1979; Strain & Mumme, 1988), confirming that song rates reflect energy balance in these species. If energy balance in turn affects an individual's ability to compete for territory, then song rates might be of interest to a singer's competitors and therefore affect the singer's success in territory defense. Song rate might also reflect an individual's motivation to compete for territory, and thus its willingness to escalate aggressively. Testosterone stimulates higher rates of singing in song sparrows and other songbirds (Ketterson, Nolan, Wolf, & Ziegenfus, 1992; Nowicki & Ball, 1989; Templeton, Burt et al., 2012) and also stimulates increased intensity of aggressive behavior (Wingfield, 1994), providing a mechanism that can link song and aggressiveness. Indeed song rate has been shown to be a reliable predictor of aggression in one other songbird, the black-capped chickadee (*Poecile atricapillus*) (Baker, Wilson, & Mennill, 2012).

Nonetheless, there is not much evidence that song rate is an important signal in territorial aggression in song sparrows. Song rates do not show consistent increases in natural aggressive contexts (Kramer & Lemon, 1983). In simulated territorial intrusions, song rates increase only gradually, so that increases tend not to be significant in response to short intrusions (Peters, Searcy, & Marler, 1980; Searcy, Nowicki, & Hogan, 2000), but are significant for longer ones (Kramer et al., 1985). Rates of songs produced at normal amplitudes (broadcast songs) do not predict whether males will attack in mount attack experiments (Akçay, Tom, Campbell, & Beecher, 2013; Searcy, Anderson, & Nowicki, 2006). No one to our knowledge has tested whether song sparrows respond to song rate in territorial playback. Presumably, song rate would have some effect in both territorial playback and speaker occupation if treatments were pushed to the extreme of very low versus very high rates, but this has not been experimentally demonstrated.

4.3. Switching Frequency

Song sparrows produce song types with eventual variety, meaning that they repeat each type multiple times before switching to another; this behavior contrasts with that of immediate variety singers, which sing only one instance of a song type before switching (Hartshorne, 1956). Birds that sing with eventual variety can vary the frequency with which they switch between song types and use switching frequency as a signal. Song sparrows possess another level of song variation—the variants within each song type—so they might also use variant-switching frequency as a signal.

Evidence from other songbird species suggests that song-type-switching frequency functions as an agonistic signal (Searcy & Beecher, 2009). In some species, males increase type-switching frequencies in aggressive contexts (Falls & D'Agincourt, 1982; Simpson, 1985), whereas in others males do just the opposite, lowering switching frequencies in aggressive contexts (Molles & Vehrencamp, 1999; Searcy & Yasukawa, 1990). Vehrencamp (2000) pointed to this pattern as strong evidence that the meaning of type-switching frequency is arbitrary with respect to its form and thus that type-switching frequency is a conventional signal.

Song sparrows fall in the category of species that increase switching frequencies in aggressive contexts. Kramer and Lemon (1983) found type-switching frequencies are lowest in males that sing by themselves, higher in males that countersing with another male, higher still immediately before a fight, and highest of all immediately after a fight. Other studies have shown that male song sparrows increase type-switching rates approximately three-fold during simulated territorial intrusions relative to undisturbed singing (Kramer et al., 1985; Searcy et al., 2000). In playback experiments, male song sparrows show a recovery in aggressive response when song types switch (Searcy et al., 1995) and show a stronger aggressive response overall to sequences that switch than to sequences that never switch (Nielsen & Vehrencamp, 1995; Stoddard et al., 1988). Type-switching thus meets two criteria needed to show that a signal is aggressive in the sense of being threatening (Searcy & Beecher, 2009): the context criterion (the signal increases in aggressive contexts) and the response criterion (aggressive rivals respond to the signal). Type-switching does not, however, meet the third, "predictive criterion": in two mount attack studies, type-switching did not predict which males would attack a taxidermic mount (Akçay et al., 2013; Searcy et al., 2006). The failure to predict aggression poses a major problem for interpreting song-type switching as a conventional signal of aggression.

Variant-switching frequencies show some of the same patterns. Variant switching in natural contexts has not been studied, but in simulated territorial intrusions, variant-switching frequency increases just as consistently as does type-switching frequency (Searcy et al., 2000). In territorial playback, male song sparrows show a recovery in aggressive response when variants switch (Searcy et al., 1995) and respond more overall to sequences of songs with variant switches than to sequences without such switches (Stoddard et al., 1988). Variant-switching frequencies again fail to predict attack in mount attack experiments (Searcy et al., 2006), just as is true for type switching. One interpretation of the accumulated evidence is that variant switching is an aggressive signal, but is not reliable enough to be of much use in predicting attack. Another interpretation is that variant switching is not a signal at all and that the different variants of a song type sung by one individual simply represent production error (Searcy et al., 2000). Production error might well increase during the stress of a territorial intrusion, providing an explanation for the observed changes in variant switching with aggressive context.

4.4. Soft Songs and Wing Waves

Nice (1943) described male song sparrows challenging an intruder as performing a "puff-sing-wave" display, in which they erect their feathers to "puff" themselves up, sing softly, that is at low amplitude, and hold up and vibrate either one wing or both. The "puff" part of this display has not been studied intensively, but the "soft song" and "wing wave" components have recently been investigated in both song sparrows and other species.

Low-amplitude song has now been noted in a considerable number of songbirds (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998; Morton, 2000; Snow, 1958; Titus, 1998). In some species, soft song is just normal or "broadcast" song produced at lower amplitudes (e.g., Hof & Hazlett, 2010), while in others soft song and broadcast song are structurally distinct (e.g., Titus, 1998). A third pattern is to add low-amplitude components to normal song (Naguib, Kunc, Sprau, Roth, & Amrhein, 2011). Song sparrows cover all these options: males produce "crystallized soft songs" which are structurally identical to song types in the normal broadcast repertoire, and "warbled soft songs," which differ from broadcast songs in temporal pattern and phonology as well as in amplitude (Fig. 3.3) (Anderson et al., 2008), and can also add soft song elements to broadcast songs. Calibrated measurements made in the field show that the distribution of song amplitudes in song sparrows is not bimodal, but instead has a single peak at high amplitude and a long tail at low amplitudes (Anderson et al., 2008). Songs subjectively categorized as broadcast songs by human observers

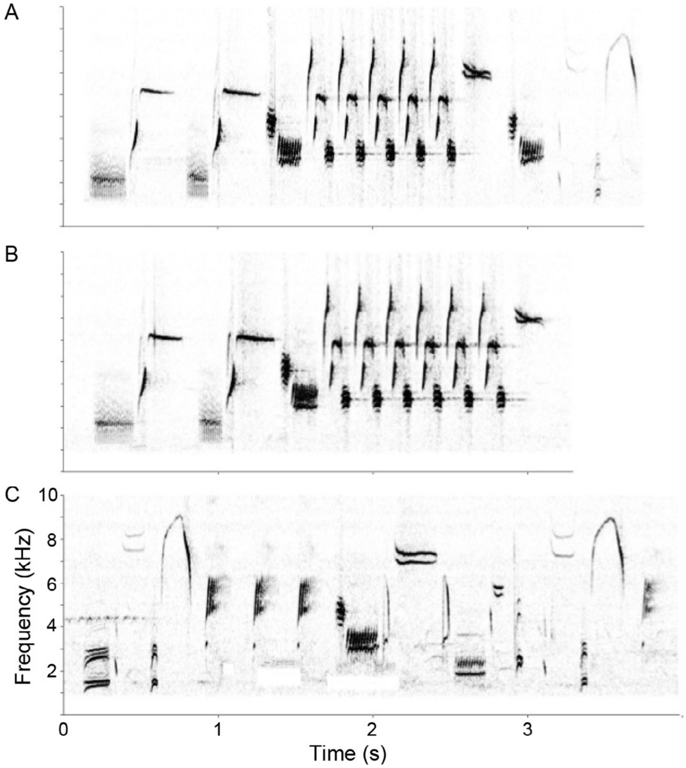

Figure 3.3 Spectrograms of (A) a crystallized soft song, (B) a normal broadcast song, and (C) a warbled soft song. All three songs were recorded from one individual. Crystallized soft songs closely resemble song types from the same male's broadcast repertoire in terms of phrase order and note composition (compare (A) and (B)), but resemble warbled soft songs in being produced at low amplitudes (Anderson, Searcy, Peters, & Nowicki, 2008). Warbled soft song do not have as regular a phrase order as crystallized soft songs and broadcast songs, and contain more high-frequency note types such as the inverted U note seen in (C) at about 0.7 s and again at about 3.3 s (Anderson et al., 2008). Note that this inverted U note does not occur in the broadcast song (B) but is added by the male to the end of the crystallized soft song (A).

have amplitudes varying from 78 to 85 dB SPL, whereas soft song amplitudes vary from 50 to 77 dB. Amplitudes are lower overall for warbled than for crystallized soft songs, but with substantial overlap (Anderson et al., 2008).

In some songbirds, soft songs are given in courtship (Dabelsteen et al., 1998; Reichard, Rice, Schultz, & Schrock, 2013), but in song sparrows soft songs have been observed only in aggressive contexts (Nice, 1943). Akçay, Tom, Holmes, Campbell, and Beecher (2011) experimentally demonstrated that song sparrows increase production of soft songs during intense aggression: during simulated territorial intrusions, territory owners produced roughly five times as many soft songs when a taxidermic mount was presented with the playback as when no mount was presented. Two mount attack experiments have found that soft song production is a strong predictor of attack. In a Pennsylvania population, Searcy et al. (2006) showed that males that eventually attacked gave more soft songs than males that did not attack and consequently numbers of soft songs could be used to predict which males would attack. Akçay et al. (2013) found very similar results in a Seattle population: more soft songs were produced by attackers than by nonattackers, and soft song production was strongly predictive of attack. In both populations, attackers gave more wing waves than nonattackers, though this trend was statistically significant only in the western population (Akçay et al., 2013) and not in the eastern (Searcy et al., 2006).

Soft songs have been shown to be reliable predictors of attack in two other songbird species: in swamp sparrows (*Melospiza georgiana*) (Ballentine, Searcy, & Nowicki, 2008), a member of the same genus as song sparrows, and in black-throated blue warblers (*Dendroica caerulescens*) (Hof & Hazlett, 2010), a member of a closely related family. Another form of low-amplitude vocalization, "soft calls," has been found to be good predictors of attack in a bird that does not sing, the corncrake (*Crex crex*) (Rek & Osiejuk, 2011), which as a member of the rail order is distantly related to song sparrows. A generalization thus seems to be emerging that low-amplitude vocalizations are especially likely to be reliable signals of aggressive intent. This generalization prompts the question: how can the reliability of such signals be maintained?

Lowering the amplitude of vocalizations should not make them more difficult to produce, so soft songs and calls are not good candidates to be performance or index signals. Low-amplitude signals are likely to have low intrinsic costs, in particular, low energy costs, so the reliability of such signals is also unlikely to be maintained by the handicap mechanism. Thus by process of elimination, receiver-dependent costs are left as the most likely explanation for the reliability of soft vocalizations as signals of aggressive intent.

What is required to maintain reliability by a receiver-dependent mechanism is that other males, especially those that are strong fighters, react with greater aggression toward soft vocalizations than toward alternative signals. Three studies have tested this prediction with respect to soft song in song sparrows. All three of the studies contrasted the response of territory owners to playback of broadcast songs and soft songs, after first using a lure song to bring subjects close enough to the speaker to be sure of hearing the soft songs. The first study gave negative results: Anderson, Nowicki, and Searcy (2007) found that male song sparrows reacted no more aggressively toward crystallized soft song than toward broadcast songs. The two later studies, however, gave positive results: Anderson, Searcy, Hughes, and Nowicki (2012) found that males reacted more aggressively toward warbled soft songs than toward broadcast songs, and Templeton, Akçay, Campbell, and Beecher (2012) found that males reacted more aggressively toward a mix of warbled and crystallized soft songs than toward broadcast songs. Taken together the studies support receiver retaliation against warbled soft song either alone or given with crystallized soft song, though not against crystallized soft song given alone.

Support for receiver-dependent costs suggests that warbled soft song in song sparrows can be viewed as a conventional signal, that is one whose meaning is arbitrary with respect to its physical design (Guilford & Dawkins, 1995). Nevertheless, a number of hypotheses have been proposed that suggest some relationship between the meaning of soft song, as a high-intensity threat, and its most obvious design feature, its unusually low amplitude. The eavesdropping hypothesis suggests that low amplitude has been favored during intense aggression to limit interception of the signal by unintended receivers, such as predators or rival males other than the one the song is directed at (Dabelsteen et al., 1998). Although this hypothesis has great intuitive appeal, experimental tests with song sparrows have not supported it. Searcy and Nowicki (2006) staged simulated intrusions on song sparrow territories with and without another stimulus, alarm calls, which indicate danger from predators. The proportion of soft songs given by subjects was actually lower in the predator context than in the control context, directly contradicting a prediction of the eavesdropping hypothesis. In a second experiment, territory owners were removed and loudspeakers placed on their territories were used to simulate interactions between each owner and an intruder. Intrusions by other males were more frequent when the simulated owner used soft song than when it used broadcast song, again directly contradicting a prediction of the eavesdropping hypothesis.

The readiness hypothesis (Akçay & Beecher, 2012; Akçay et al., 2011) is a second attempt to explain why low amplitude characterizes highly aggressive vocalizations. This hypothesis suggests that low amplitude is a byproduct of the posture a bird assumes in order to minimize its vulnerability to a nearby opponent. In particular, when delivering soft song the head is held level so that the opponent can be tracked visually, whereas throwing the head back may be necessary to generate greater amplitude (though this has not been demonstrated explicitly). Under this hypothesis, the acoustic property that defines soft song (low amplitude) is not arbitrary with respect to its meaning. Neither the readiness hypothesis nor the eavesdropping hypothesis explains the reliability of the signal, and here a receiver retaliation cost remains the most likely hypothesis.

Although soft song is the most reliable aggressive display known in song sparrows, its reliability is nevertheless limited, in the sense that its association with subsequent aggressive behavior is imperfect. Searcy et al. (2006) and Akçay et al. (2013) found that the number of soft songs given per unit time by male song sparrows correctly predicted whether a male would attack a mount for 74% and 67% of subjects, respectively, meaning that attack was not correctly predicted in about one quarter and one third of individuals. Limited reliability for aggressive signals is not surprising, as game theory analyses have traditionally assumed that signalers are often selected to bluff by oversignaling relative to their actual level of aggressiveness (Caryl, 1979; Maynard Smith, 1974, 1979). Searcy, Anderson, Ballentine, and Nowicki (2013), however, showed that most male song sparrows give few or no soft songs and that "undersignaling" is actually more common than is "oversignaling." Akçay et al. (2013) found that about half the males that attacked did not give high rates of soft song, whereas only 12% of non-attackers had high rates of soft song, which again implies that undersignaling is more common than is oversignaling. Akçay, Campbell, and Beecher (2014) have recently shown that male song sparrows are individually consistent in whether they oversignal or undersignal. Consistent oversignaling can be accounted for as bluffing, but consistent undersignaling is more difficult to explain. One possibility is that individuals that are especially confident of their fighting ability attack without bothering to waste time in signaling (Searcy, Anderson, et al., 2013).

Receiver response to wing-waving has not been investigated in song sparrows, but has been studied in the closely related swamp sparrow, where this display is also a reliable predictor of attack (Ballentine et al., 2008). Male swamp sparrows reacted more aggressively toward a robotic swamp sparrow mount when it wing-waved than when it did not (Anderson, DuBois, Piech, Searcy, & Nowicki, 2013), suggesting that reliability of wing-waving may also be maintained by receiver dependent costs.

4.5. Song-Type Matching

Song-type matching is a behavior in which one singer replies to another with the same song type that the other has just sung. Given sharing of song types, two individuals with moderate-sized repertoires (such as song sparrows) will match each other at appreciable frequencies just by chance. In a number of songbird species, however, it has been shown that males match at frequencies considerably higher than chance levels, both in natural interactions (Burt & Vehrencamp, 2005; Gammon, Hendrick, & Baker, 2008; Rogers, 2004) and in response to playback (Falls, 1985; Krebs, Ashcroft, & Van Orsdol, 1981; Price & Yuan, 2011; Schroeder & Wiley, 1983). Many songbirds thus appear to match each other "intentionally," though whether a conscious decision to match is made of course cannot be stated.

Stoddard, Beecher, Campbell, and Horning (1992) found that male song sparrows matched playback of one of their own songs (self song) at a frequency of 0.60, well above the chance level, which was estimated as 0.125 from the reciprocal of the mean repertoire size. Other studies also have found that male song sparrows match self songs at high frequencies (Anderson, Searcy, & Nowicki, 2005; McArthur, 1986). Stoddard, Beecher, et al. (1992) found that the frequency of matching in response to a shared stranger song (0.50) was slightly lower than to self song but still significantly above chance, and that the frequency of matching of a shared neighbor song played from the neighbor's boundary was low (0.20) and not significantly above chance. A subsequent study (Beecher, Campbell, Burt, Hill, & Nordby, 2000) confirmed that matching was low to songs of established neighbors, but found high levels of matching (0.73) to songs of newly established neighbors.

Beecher, Stoddard, Campbell, and Horning (1996) described a second form of matching in song sparrows, which they termed "repertoire matching." Here, a male replies to a neighbor with any song type shared between their repertoires (Fig. 3.4). In the original study of repertoire matching, the chance expectation of a repertoire match was quite high (0.42) because of the high level of song-type sharing in the Seattle population under study; nevertheless, the observed frequency of repertoire matches in response to playback of neighbor song (0.875) was significantly higher than chance (Beecher et al., 1996). Repertoire matching at above chance levels was later confirmed in a second study of the same Seattle population (Beecher, Campbell, Burt, et al., 2000). Song sparrows were found to be as likely to repertoire match when played an unshared neighbor song as when played a shared song (Beecher et al., 1996), so repertoire matching provides a mechanism of addressing a song to a neighbor whether or not the neighbor has sung a shared song.

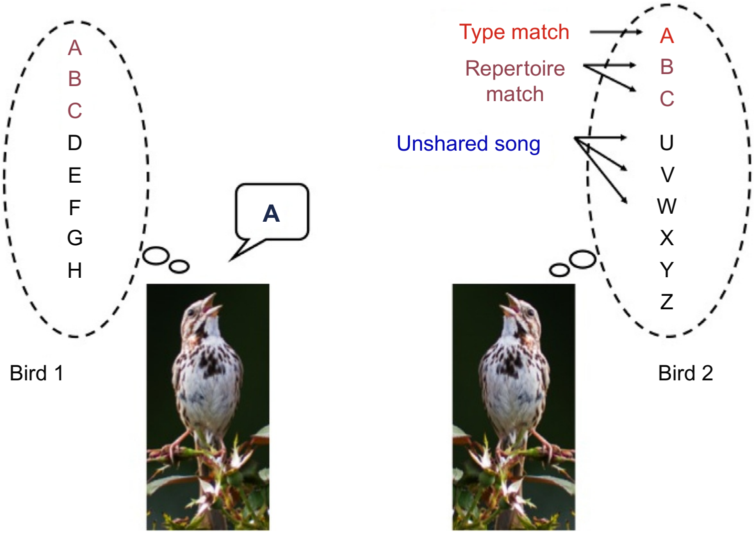

Figure 3.4 Song-type matching and repertoire matching in song sparrows. Some of male 2's song types are shared with male 1 (A, B, and C) but others are unshared (U, V, W, X, Y, and Z). If male 1 sings a shared song (e.g., A), male 2 can type match by replying with the same song type or he can repertoire match by replying with another shared song (B or C). If male 1 sings an unshared song (e.g., D), male 2 cannot type match but can still repertoire match by singing a shared song (A, B, or C).

Both type matching and repertoire matching require that pairs of neighbors share songs. Several studies have reported levels of song sharing in various song sparrow populations, but unfortunately methodological differences hamper comparisons between them. Some authors have reported the level of sharing between one male and any other male that was recorded, giving results that are highly dependent on sample size (Eberhardt & Baptista, 1977). We focus here on studies that report the frequency of sharing between pairs of adjacent neighbors (Table 3.1), a measure that is not sample size dependent, though even in these studies there is variation in the criteria used to decide whether two songs are similar enough to be considered shared.

It is clear from Table 3.1 that the level of whole-song sharing varies widely between song sparrow populations, from a high of 37% to a low of 3%. Migratory status predicts sharing in comparisons across songbird species (Handley & Nelson, 2005), but does not do so for song sparrow populations. Note, in particular, that the highest level of sharing occurs in the Gold Creek population, a high-altitude population that must totally vacate its breeding area for half the year because of snow cover (Hill

Table 3.1 Levels of Whole Song Sharing Between Pairs of Adjacent Neighbors in Various Song Sparrow Populations

Authors	Location	Migratory Status	Whole-Song Sharing (%)
Cassidy (1993)	Mandarte Island, British Columbia (West)	Nonmigrants	32
Hughes, Nowicki, Searcy, and Peters (1998)	Hartstown, Pennsylvania (East)	Partial migrants	3
Hill, Campbell, Nordby, Burt, and Beecher (1999)	Seattle, Washington (West)	Nonmigrants	24
Hill et al. (1999)	Gold Hill, Washington (West)	Altitudinal migrants	37
Wilson, Towner, and Vehrencamp (2000)	San Diego, California (West)	Nonmigrants	17
Foote and Barber (2007)	Nova Scotia (East)	Partial migrants	33

et al., 1999). Although these altitudinal migrants may not move far compared to latitudinal migrants, they do move far enough that all association between neighboring territory owners must be disrupted for at least part of the year. Note also that a simple east/west geographic difference is not supported, given the contrast in sharing between the two easternmost populations, in Pennsylvania (3%) and Nova Scotia (33%).

In a population with low song sharing, such as the Pennsylvania population just mentioned, relatively few males share whole-song types with any of their adjacent neighbors, which would seem to minimize the possibility of interaction through song-type matching. Burt, Bard, Campbell, and Beecher (2002), however, showed that male song sparrows match at frequencies well above chance playback of songs whose only resemblance to one of their own song types is a rough similarity in the form of their introductory phrases. In the Pennsylvania population with just 3% whole-song sharing, sharing of parts of songs, particularly of introductory phrases, is comparatively common (Hughes et al., 1998). Anderson et al. (2005) found that males in this Pennsylvania population matched playback of songs sharing only their introductory phrases on 57.5% of trials, just as often as they matched wholly shared songs. Thus, low sharing of whole songs does not preclude widespread interaction through forms of song-type matching.

Song-type matching has been suggested to be an aggressive signal, that is a threat in songbirds, in general (Krebs et al., 1981). For song sparrows, a more specific hypothesis has been proposed, in which song-type matching represents an intermediate level of threat in a hierarchical signaling system (Akçay et al., 2013; Beecher & Campbell, 2005; Searcy & Beecher, 2009). In the proposed model (Fig. 3.5), an interaction between two neighbors begins with one of them singing a shared song type. The focal male can then reply with (1) a song-type match, signaling escalation, (2) a repertoire match, signaling no change in the level of aggression, or (3) an unshared song type, signaling de-escalation. As the focal male continues singing, he has a choice of either staying on the match, which sustains escalation, or switching off the match, which deescalates. If the rival male does not back down, the focal male can further escalate from type matching to giving soft songs and wing waves; the latter two displays signal that an attack is imminent.

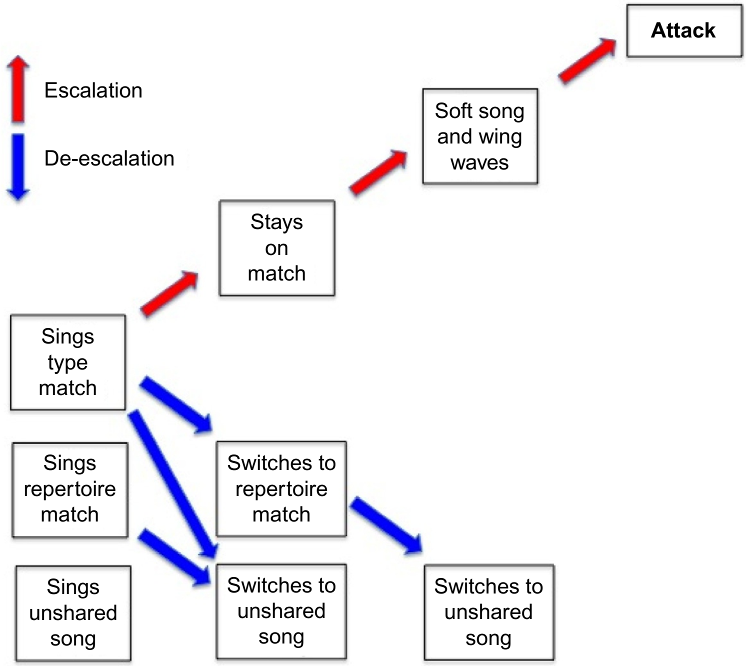

Figure 3.5 A model of hierarchical aggressive signaling in song sparrows. The upper chain of signals connected with arrows angled upward shows a typical series of escalating moves that might be made by one male leading up to an attack on a rival. The moves connected with downward arrows show some (but not all) of the deescalating transitions that are possible. *Adapted with modification from Beecher and Campbell (2005), Searcy and Beecher (2009), and Akçay et al. (2013).*

Considerable evidence supports the hierarchical signaling model for the western population of song sparrows studied by Beecher, Akçay, and colleagues. In this Seattle population, males show a stronger aggressive response toward a song-type match than toward a repertoire match (Burt, Campbell, & Beecher, 2001); this result together with the fact that males tend to type match new neighbors and repertoire match established neighbors supports the idea that repertoire matching is lower in the hierarchy of threats than is type matching. Akçay et al. (2013) tested further predictions of the model in a two-part playback design, in which territory owners were first given the opportunity to type match playback at a boundary, and then were subjected to a second playback coupled with presentation of a taxidermic mount at the center of the territory. Two results strongly supported the model. First, matching and staying on the match predicted attack on the mount though not as reliably as soft song and wing waves. Second, matching and staying on the match predicted production of one of the higher level threats, wing waves. Thus type matching seems to function as an intermediate level of threat in this population—more threatening than a repertoire match or a nonmatch, but less threatening than wing waves and soft song.

A different picture has emerged in the eastern population studied by Searcy, Nowicki, and colleagues. In this Pennsylvania population, type matching did not predict attack in a mount attack experiment (Searcy et al., 2006). In a two-part edge/center playback study, similar to that performed by Akçay et al. (2013), Searcy, DuBois, Rivera-Caceres, and Nowicki (2013) found that matching at the territory edge was not associated with greater aggressive response to playback at the territory center and was not predictive of soft songs or wing waves. Individuals in this population are consistent in their aggressive responses from trial to trial (Hyman, Hughes, Searcy, & Nowicki, et al., 2004; Nowicki, Searcy, Krueger, & Hughes, 2002; Searcy, DuBois, et al., 2013), but are not consistent in whether they match (Anderson et al., 2005; Searcy, DuBois, et al., 2013), which precludes a strong relationship between matching and aggressiveness. Thus, in the Pennsylvania population, type matching does not function as an intermediate level of threat as suggested by the hierarchical signaling model. Repertoire matching has not been investigated in this population.

Another difference between the Seattle and Pennsylvania populations is in the association between song-type sharing and male fitness. Beecher, Campbell, and Nordby (2000) measured neighborhood sharing in the Seattle population as the number of songs shared by a focal male with neighbors holding territories adjacent or one territory removed. For 45 focal males, neighborhood sharing in the first year of breeding was positively correlated with territory tenure, that is with the number of years that a male kept his territory ($r=0.43$, $P=0.003$). Neighborhood sharing was positively correlated with the focal male's repertoire size, but the correlation between sharing and territory tenure was not diminished when repertoire size was held constant ($r=0.47$, $P=0.002$). In a second western population (in San Diego), Wilson et al. (2000) found a significant positive association between average song-type sharing with adjacent neighbors and the probability of surviving to the next breeding season. One needs to be cautious, however, in interpreting these correlations, as they may not imply a causal relationship between sharing and fitness. Instead of song sharing causing longer tenure, it may be, for example, that young birds that establish good relationships with their older neighbors are more likely to learn songs from them and then experience longer tenure because of their good relationships rather than because of sharing songs.

Hughes, Anderson, Searcy, Bottensek, and Nowicki (2007) examined associations of sharing with territory tenure in their Pennsylvania study population, using the same measure of neighborhood sharing employed by Beecher, Campbell, and Nordby (2000). Neighborhood sharing was significantly lower in the Pennsylvania population than in Seattle, as would be expected from the lower level of sharing between pairs of adjacent neighbors (see Table 3.1). For a sample of 55 males, territory tenure was not associated with neighborhood sharing ($r=0.030$, $P=0.828$). Sharing of introductory phrases was more common than sharing of whole songs in Pennsylvania and was just as common as sharing of introductory phrases in Seattle. Nevertheless, sharing of introductory phrases with neighbors was not associated with territory tenure in Pennsylvania ($r=0.027$, $P=0.847$).

Synthesizing the results on matching and sharing in the two best-studied populations of song sparrows, a fairly coherent picture emerges. In Seattle, both song-type matching and repertoire matching have important signaling functions in communicating intermediate and low levels of threat, respectively. Perhaps as a consequence of the importance of matching as a signal, song-type sharing, which is necessary for both kinds of matching, is positively associated with a male fitness measure, the length of territory tenure. And perhaps as a consequence of the importance of sharing to fitness, the song-learning strategy of males is adapted to promote song sharing between neighbors and levels of sharing between neighbors are high. In Pennsylvania, by contrast, song-type matching does not function as a threatening signal and no other function has been demonstrated. Whether males in this population repertoire match at all is unknown. Given the lesser importance of matching as a signal, it is not surprising to find that song-type sharing is not associated with male fitness. And given the lesser importance of song sharing to male fitness, it seems logical to find that levels of song sharing are low. Low levels of sharing in Pennsylvania may be a consequence of a song-learning strategy that differs from that found in Seattle in deemphasizing learning of whole songs, but this hypothesis needs to be tested with a common garden experiment using hand-reared birds (Beecher, 2008).

What does not seem logical in the above scenario is that though song-type matching seems less important as a signal in Pennsylvania than in Seattle, males nevertheless type match in response to playback just as frequently in Pennsylvania (Anderson et al., 2005; Searcy et al., 2006, Searcy, DuBois, et al., 2013) as in Seattle (Akçay et al., 2013; Burt et al., 2002; Stoddard, Beecher, Campbell, et al., 1992). It is possible that matching has some function in Pennsylvania other than in signaling aggression (Logue & Forstmeier, 2008; Nelson & Poesel, 2013), but if so then the low frequency of sharing in Pennsylvania would be unexplained. It is also possible that matching occurs in Pennsylvania as a phylogenetic holdover from a common ancestor with western song sparrows.

5. DEAR-ENEMY RELATIONS

The term "dear enemies" was coined by James Fisher to describe neighboring territory owners who, though competitors, nevertheless enjoy relatively amicable relations (Fisher, 1954). Studies have subsequently shown that territory owning birds indeed often exhibit lower aggression toward neighboring territory owners than toward owners of more distant territories (strangers) (Stoddard, 1996; Temeles, 1994; Weeden & Falls, 1959). Exceptions are known, however, where the opposite pattern is found (Müller & Manser, 2007; Temeles, 1990). Dear-enemy relationships have been demonstrated in a variety of animals in addition to songbirds, ranging from invertebrates (Langen, Tripet, & Nonacs, 2000; Pfennig & Reeve, 1989) to fish (Leiser & Itzkowitz, 1999), amphibians (Jaeger, 1981), reptiles (Husak & Fox, 2003), and mammals (Rosell & Bjørkøyli, 2002).

Two classes of hypotheses have been proposed to explain the occurrence of dear-enemy relationships (Booksmythe, Jennions, & Backwell, 2010; Temeles, 1994). One class is based on familiarity: neighbors are suggested to be familiar with each other's fighting ability and likelihood of winning, so that prolonged and escalated fighting is not needed to settle a dispute (Getty, 1989; Ydenberg, Giraldeau, & Falls, 1988). The second class is based on relative threat: neighbors are judged to be less of a threat to a territory owner than is a stranger, in large part because neighbors are known to have their own territories, and are therefore less likely to attempt a takeover than are strangers, whose territorial status is often not known (Getty, 1987; Temeles, 1994). Variation in relative threat has been more successful than variation in familiarity in explaining the exceptions in which the dear-enemy phenomenon does not hold (Temeles, 1990, 1994), strengthening the case for the relative threat hypotheses overall.

Four studies of dear-enemy relations have been conducted with song sparrows, all based on the same general experimental design: songs of neighbors and songs of strangers are played separately to a subject and the strength of the aggressive response to both is observed. All four studies have found that owners show greater aggression toward stranger song than toward neighbor song, but the strength of neighbor/stranger discrimination has varied, with weak discrimination in three studies of eastern populations (Harris & Lemon, 1976; Kroodsma, 1976; Searcy, McArthur, Peters, & Marler, 1981), and strong discrimination in one study of a western population (Stoddard, Beecher, Horning, & Willis, 1990). Stoddard et al. (1990) attributed the difference in results to a specific difference in methods: in their tests of a western population, they placed the playback speaker on the neighbor's territory, just across the boundary from the subject's territory, whereas all three tests with eastern populations placed the speaker on the subject's territory, somewhere near the boundary with the neighbor (Harris & Lemon, 1976; Kroodsma, 1976; Searcy et al., 1981). Another possibility is that song sparrows actually have stronger dear-enemy relationships in western than in eastern populations.

Neighbor/stranger discrimination, whether weak or strong, requires that territory owners be able to distinguish neighbors as a class from strangers as a class by song alone. Stoddard et al. (1991) demonstrated that territory owners in song sparrows can go beyond recognizing categories of males to recognizing specific individuals. Adapting the classic experimental design of Falls and Brooks (1975), Stoddard et al. (1991) presented neighbor and stranger songs from three sets of locations: (1) from the center of the subject's territory, (2) from just across the boundary on the neighbor's territory, and (3) from the opposite boundary. Subjects showed lower aggressive response to neighbor song than to stranger song only for the second set of sites, where songs were played from the neighbor's own territory. At the other sites, owners responded just as aggressively to neighbor song as to stranger song. The results, then, show that owners associate a song with the specific neighbor that sings it, thus demonstrating individual recognition. The results also support relative threat explanations of the dear-enemy phenomenon over familiarity hypotheses, as moving the apparent position of the neighbor should not change its familiarity, but may well change the level of threat it offers.

Individual recognition of neighbors allows song sparrows to follow a conditional strategy of cooperation, which provides a mechanism for maintaining dear-enemy relations. The idea is that two neighbors cooperate by each respecting the other's territory, with cooperation enforced by the threat of retaliation if the other defects (Getty, 1987; Godard, 1993). Akçay et al. (2009) experimentally demonstrated that song sparrows retaliate in the predicted way (Fig. 3.6). The experiment began with the simulated intrusion of one neighbor on the subject male's territory, using playback of one of the neighbor's songs. After a lapse of 45 min, the subject was presented with two boundary playbacks in random order, one from the "bad neighbor," whose intrusion had previously been simulated, and the other from an unoffending "good neighbor." Subjects were much more aggressive toward the bad neighbor. Owners thus remember which neighbor has

Figure 3.6 An experimental test for direct reciprocity in territorial defense. (A) The experimental design. In (1), playback of song is used to simulate an intrusion by one neighbor on the subject's territory, making this the "bad neighbor." Subsequently, the subject is played (in random order) song recorded from the bad neighbor (2a) and from an unoffending "good neighbor" (2b) from their respective boundaries. (B) Results. Subjects respond on average much more aggressively to bad neighbors than to good neighbors.

(seemingly) defected from cooperation and retaliate against him with greater aggression. Retaliation against defecting neighbors has also been found in some other songbirds (Godard, 1991; Olendorf, Getty, Scribner, & Robinson, 2004) but not all (Hyman, 2002).

The bad neighbor experiment illustrates a form of direct reciprocity, in which A's treatment of B depends on how B has treated A. In theory, cooperation can also be maintained by indirect reciprocity, in which A's treatment of B depends not on how B has treated A but on how B has treated other individuals (Nowak & Sigmund, 1998). Indirect reciprocity has seldom been demonstrated in nonhuman animals, but song sparrow territoriality provides one good example. Akçay, Reed, Campbell, Templeton, and Beecher (2010) used song playback to simulate the intrusion by a neighbor (the defector) of a focal male onto the territory of a second neighbor (the victim) (Fig. 3.7). After a lapse of 30 min, two boundary playbacks (in

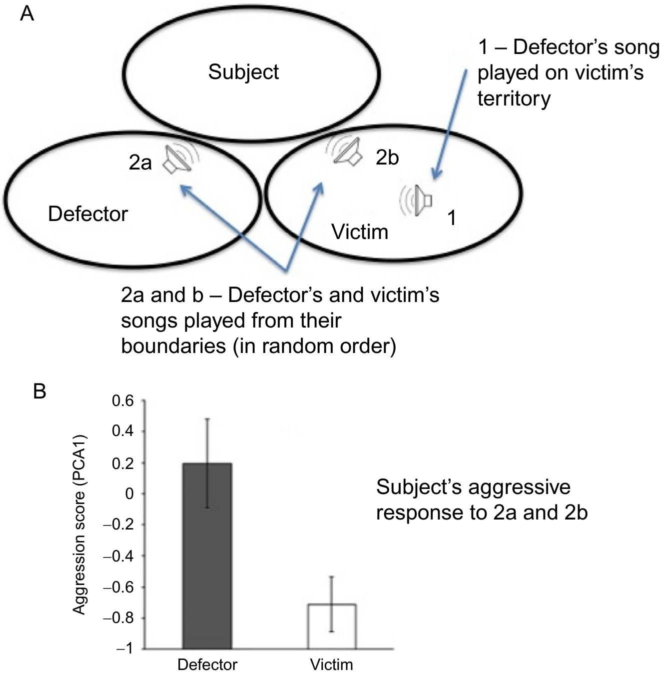

Figure 3.7 An experimental test for indirect reciprocity in territorial defense. (A) The experimental design. In (1), playback of song from one neighbor (the "defector") is staged on the territory of another neighbor (the "victim"). Subsequently the song of the defector (2a) and the song of the victim (2b) are played (in random order) from their respective boundaries. (B) Results. Subjects respond on average much more aggressively toward defectors than toward victims.

random order) were used to test the reaction of the focal male to the defector and to the victim. Subjects showed significantly stronger aggression toward the defector than toward the victim, with response differentials similar to those seen in the experiment on direct reciprocity. In other words, territory owners retaliated about as strongly against a neighbor who violated the territory of another neighbor as against a neighbor who violated their own territories.

Song sparrows can be viewed as cooperating in territory defense, but it is cooperation of a limited kind: cooperation through mutual forbearance. A more active form of cooperation would be for neighboring territory owners to join together in driving away outsiders. Systematic studies of this type of cooperation have not been undertaken in song sparrows.

6. CONCLUSIONS

Much of what has been discovered about aggressive signaling in song sparrows fits well with theory and with what has been discovered about territorial signaling in other animals. Song sparrows possess displays that reliably signal aggressive intentions, notably soft song and wing waves. These displays can probably be classified as conventional signals, with meanings that are arbitrary with respect to their physical form, and with reliability enforced by receiver-dependent costs. Low-amplitude vocalizations such as the soft song of song sparrows are emerging as a class of signals that are especially likely to be used to signal high levels of threat, at least across birds. In one intensively studied population (Seattle), song sparrows have a hierarchy of aggressive signals, allowing them to communicate a graded series of threats. Territory owners in song sparrows maintain dear-enemy relations with their neighbors. The same is true in many species of territorial animals, but the mechanisms are especially well understood in song sparrows. These mechanisms are predicated on the ability of song sparrows to recognize others as individuals and involve both direct and indirect reciprocity.

What has emerged as the most unexpected aspect of song sparrow aggressive signaling is the existence of geographical variation not just in signal form but in how the signaling system functions. Robust evidence exists for three aspects of variation in the territorial signaling system of song sparrows: (1) variation in the frequency of song-type sharing between neighbors; (2) variation in the relationship between song-type sharing and male territory tenure; and (3) variation in the importance of song-type matching as an aggressive signal. These three axes of variation are related in a way that makes evolutionary sense, but further work is needed before the patterns are fully understood. In the meantime, the existence of such geographic differences in the function and meaning of a single species' signals should serve as a cautionary note in interpreting the signals of other species that have been studied at only a single locality.

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