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The role of unshared songs in singing interactions between neighbouring song sparrows

MICHAEL D. BEECHER & S. ELIZABETH CAMPBELL
Animal Behavior Program, Departments of Psychology and Biology, University of Washington

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In this paper we focus on the potential advantage song repertoires may provide in singing interactions between two birds. We have previously shown that neighbouring song sparrows, *Melospiza melodia*, in our population countersing with shared songs: a bird escalates an interaction by replying with the same song type his neighbour just sang ('type matching'), or sends a directed but less threatening signal by replying with a different but still shared song ('repertoire matching'). In the present study we tested and confirmed two predictions: (1) that a bird would be more likely to perceive a neighbour's song as directed at him if it was shared than if it was unshared; (2) that an unshared song would be a more effective de-escalation signal than a shared song. In the first of two playback experiments, subjects responded with shorter latencies to neighbours' shared songs than to their unshared songs. In the second, 'interactive' playback experiment, a playback trial began when the subject sang a shared song type. We replied with the neighbour's matching type (an escalation signal), until the subject approached, and then switched to either a different shared song (a 'repertoire match') or to an unshared song. As predicted, subjects responded less aggressively and departed sooner when the switch was to an unshared song than when it was to a shared song.

In most songbirds, individual birds sing not one but many different species-specific songs (i.e. have 'song repertoires'). Many theories have been proposed to explain the adaptive advantage of song repertoires (see reviews in: Searcy & Andersson 1986; Catchpole & Slater 1995). Most of these theories have held that the different songs in the repertoire convey only one basic message, 'I am an adult male of the species in possession of a territory', and that the advantage of a repertoire lies in the diversity that different songs provide. For example, according to one theory, by repeatedly changing the song he is singing, the bird reduces habituation and maintains the listener's attention (Hartshorne 1956; Kroodsma 1988). This argument has been made for both inter- and intrasexual contexts (Kroodsma 1983; Searcy & Yasukawa 1990).

In this paper, we suggest a different (but not mutually exclusive) perspective. We present a model of how songbird neighbours might use their long-distance signals (songs) to modulate territorial interactions. The model is based on a corollary of the 'dear enemy' hypothesis (Getty 1987; Temeles 1994). According to the dear enemy hypothesis, long-term neighbours are preferred to new neighbours because new neighbours are inherently expansionist while long-term neighbours generally respect territory boundaries once they have been established. An obvious corollary, then, is that established neighbours should use long-distance signals in place of time- and energy-costly physical interactions to minimize territorial conflicts.

In our model, the key dimension differentiating songs in a bird's repertoire is their similarity to the neighbour's songs. We divide the songs in two neighbours' repertoires into two classes, similar (i.e. types 'shared' by the two birds) and dissimilar (i.e. 'unshared', although these types might be shared with other birds). In truth, songs may vary on a continuum of similarity, but for convenience in this paper we will describe them as similar or dissimilar (shared or unshared) as has been conventional in this area. The model is depicted in Fig. 1, which shows the focal bird initiating a singing interaction with his neighbour, the neighbour responding, and the focal bird replying to the neighbour. In the first phase, the focal bird engages his neighbour by singing a song they share. In the second phase, the neighbour can escalate, maintain or de-escalate the interaction by his reply to the neighbour's song. He can escalate the interaction by replying

Correspondence: M. D. Beecher, Box 351525, University of Washington, Seattle, WA 98195, U.S.A. (email: beecher@u.washington.edu).

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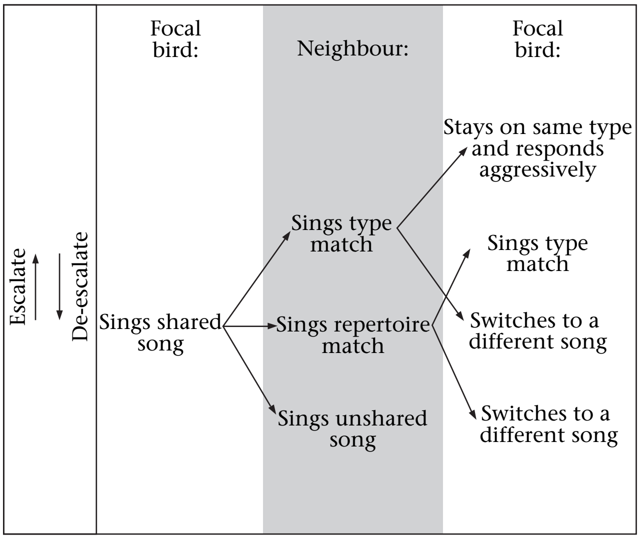

Figure 1. Diagram of singing interactions between a focal bird and his neighbour, who share song types. Escalation is indicated by behaviours higher in the diagram, and de-escalation by behaviours lower in the diagram. In this figure, the interaction begins when the focal bird sings a shared song type. The neighbour can then either type-match the focal bird (an escalation), repertoire-match (a directed but neutral signal) or sing an unshared song (a de-escalation). If the focal bird 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 (the diagram does not reiterate that this different song type may be either a repertoire match or an unshared song). Aggressive response refers to searching for, threatening or attacking the singer.

with the same song type ('type matching'), a signal that he will escalate if the focal bird escalates (e.g. moves closer to or crosses the territory boundary). He can maintain the interaction at the same level by replying with another but different song they share ('repertoire matching'). He can de-escalate the interaction by replying with a song they do not share. In the third phase, if type-matched, the focal bird can escalate further by staying on type (in which case the birds will be close to an actual fight; Burt et al. 2001), or de-escalate by switching off type (switching to an unshared type would be more of a de-escalation than switching to a shared song). If the focal bird had been repertoire-matched, it could escalate by type matching or de-escalate by switching to an unshared song. The particular reply choices the birds make are dependent on context and history. For example, early in the season, a new neighbour singing near a boundary that the two birds have been disputing will probably elicit a type-match from the subject ('back off or I'll come after you'). The same stimulus later in the season, or from a long-term neighbour, should elicit a milder repertoire match (individually directed, but nonthreatening). Finally, a bird feeding nestlings might choose to break off the interaction expeditiously by replying with an unshared song type.

We have tested and confirmed our predictions concerning type and repertoire matching in a series of playback experiments (Beecher et al. 1996, 2000a; Burt et al. 2001, 2002). In all of these experiments, we simulated a neighbour singing by playing his song to the subject from just on the neighbour's side of their mutual border. We began a playback trial when the neighbour was far away and not singing and we used a directional loudspeaker (see Methods) so that the actual neighbour did not hear the broadcast (his own) song; if he did hear the broadcast and approached the playback speaker during the trial, we terminated and threw out that trial. For our experiments we used neighbours who shared 2–5 of their 8–9 songs, as is typical of most neighbours in our study population. In our first study in this series, we showed that a song sparrow, *Melospiza melodia*, in our population generally does not reply to the shared song of a long-term neighbour with that song type (type matching) but instead replies with a different song type he shares with that neighbour (repertoire matching; Beecher et al. 1996). In contrast, if the neighbour is a new one and it is still early in their first breeding season as neighbours, a bird will type-match a shared song (Beecher et al. 2000a). These results are consistent with our model, specifically with the hypothesis that repertoire matching is a directed response to the neighbour but one with lower threat value than song type matching.

Additional evidence that type matching is threatening, as originally proposed by Krebs et al. (1981), and that repertoire matching is less so, is provided by a recent interactive playback experiment (Burt et al. 2001). In this experiment, when the subject sang a song shared with a neighbour, we simulated the neighbour issuing a song reply, either a type match or, on a different day, a repertoire match. Song sparrows responded to the neighbour song playback more aggressively when it was a type match than when it was a repertoire match, supporting the prediction that birds on their own territory will perceive a type match from a neighbour as a challenge and will be more likely to escalate. Moreover, some subjects responded more strongly than others when type-matched, and those who did continued to sing the matching type throughout the trial, whereas those who responded more weakly either switched types or stopped singing. Thus, replying to a neighbour with the same song type is both a signal of and a predictor of aggressive response.

Figure 1 contains an additional hypothesis not tested in Burt et al. (2001), which we test in the present study: that a singer can de-escalate an interaction by singing an unshared song. That is, according to the model, when the focal bird sings a shared song, the neighbour can choose to escalate the interaction by replying with the same type (type matching), de-escalate by replying with an unshared type, or respond at an intermediate level by replying with a different shared type (repertoire matching). In turn, the focal bird can escalate the interaction by replying to a repertoire match with a type match, but he cannot do so when the neighbour sings an unshared type.

In the present study we examined the role of unshared songs in neighbour singing interactions. We tested two predictions. (1) According to our model, when a bird commences to sing on his territory, he can direct his song to a specific neighbour by choosing a song they share (as well as by singing near their common boundary and singing towards the neighbour). Therefore in our first experiment, we tested whether the subject would indeed respond with a shorter latency to a neighbour singing a shared (versus an unshared) song. (2) According to our model, once neighbours are in a countersinging interaction, a bird can de-escalate an interaction by singing an unshared song. Therefore in our second experiment, we used an interactive playback design to test whether an unshared song was more effective than a shared song at ending an interaction. Specifically, we waited for the subject to begin singing a song shared with the focal neighbour. We then simulated that neighbour replying to the subject with the same song type (i.e. type matching, an escalation signal). When the subject responded by approaching the playback, we switched to either an unshared song or (on a different day) a different shared song. According to the model, singing an unshared song is an unambiguous de-escalation signal, whereas repertoire matching is an intermediate signal. Therefore, we predicted that the subject would break off the interaction more quickly if the neighbour song playback switched to an unshared song than if it switched to another shared song.

METHODS

Study Area and Subjects

Our song sparrow study site is an undeveloped 3-km^2 park bordering Puget Sound in Seattle, Washington, U.S.A. The song sparrow population is nonmigratory, with approximately 150 males on territories in a given year. For the two playback experiments, we used as subjects 25 banded territorial males who were at least 1 year old. Before the experiment we recorded the full song repertoires of each subject. A male served both as a subject and as a source of stimulus songs for trials on his neighbour. Neighbour pairs were selected at random from the population, the only requirement being that they share at least two song types. Subject repertoire sizes ranged from 7 to 12 song types (mean 9.1) and the percentage of songs shared between pairs ranged from 30 to 80% (mean 56%).

Recording, Playback and Song Type Analysis

Song repertoires of the subjects were recorded in the field with a Sennheiser ME88 directional microphone and a Sony TC-D5M tape recorder. We estimated a repertoire to have been completely measured (all song types) when we had recorded 20 or more consecutive song type switches (method and rationale described in Kroodsma 1982). Songs were analysed with the program ‘Syrinx’ (written by John M. Burt, www.syrinxpc.com). Two songs were considered to be matches if they shared 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, which are more variable and less important in individual recognition (Nice 1943; Horning et al. 1993). An example is shown in Fig. 2: we classified the song pairs in the top three rows as shared songs, and the six songs in the bottom three rows as unshared songs (omitted from the figure are several other unshared songs of the two birds).

Playback songs were presented using a Dell Latitude LT laptop computer with a 16-bit sound card, attached to an amplified speaker via a 10-m cable. Playback songs were digitized in 16 bits at a 22 050-Hz sample rate. The program Syrinx allowed us to display playable spectrograms of all song types in the repertoires of the subject bird and his neighbour. The Syrinx program also displayed a real-time spectrogram of the song that the subject was singing, using a directional microphone as input to the computer. In the interactive experiment, this set-up allowed us to quickly identify the subject’s song type, and select and play the appropriate stimulus song. In both experiments, we recorded all songs that the bird sang as well as a verbal record of the subjects’ behaviours (other vocalizations, flights, threat displays, etc.); the field computer stored and kept a real-time record of all of these events.

During a playback trial the subject’s neighbour might hear and respond to the playback by approaching or singing, in which case the trial had to be aborted. To reduce the likelihood of a neighbour’s appearance, we used a highly directional speaker consisting of a Radio Shack enclosed midrange tweeter (M 40-1289A, frequency range 200–20 000 Hz), attached with the speaker output at the focal point of a Sony parabolic reflector. The apparatus was mounted on a tripod and could be aimed at a subject bird with minimal sound heard behind it (in the neighbour’s direction). Peak playback sound levels were approximately 75 dB SPL (C-weighting) at 10 m in front of the speaker with 35–40 dB attenuation from the peak level at 10 m directly behind the speaker. Playback levels were chosen to approximate the natural levels of a singing bird.

Playback Conditions and Procedure

General procedures

The two experiments were carried out in 2000 and 2001. Trial dates in 2000 ranged from 19 April to 27 June, and in 2001, from 24 April to 27 June, with trials conducted in the morning between 0700 and 1100 hours. The birds (which had multiple clutches) were in various phases of the breeding cycle (starting a clutch, incubating, feeding nestlings, feeding fledglings). For each subject, trial type order was randomly determined, and only one trial was administered per day. Neighbours were occasionally tested on the same day, but always with at least a 2-h delay between trials.

Experiment 1 (passive)

Before the trial, we set our playback speaker to broadcast towards the subject from just within the neighbour’s side of their contiguous territorial boundary. We did not begin a trial until the subject and the neighbour had both been quiet for at least 1 min and well away from the territory boundary. The playback stimulus was either a song that the two birds shared or (on another day) a song that they did not share; the trial order was counterbalanced across subjects. A trial lasted 3 min, starting from the first playback. Playback occurred with 10-s pauses between

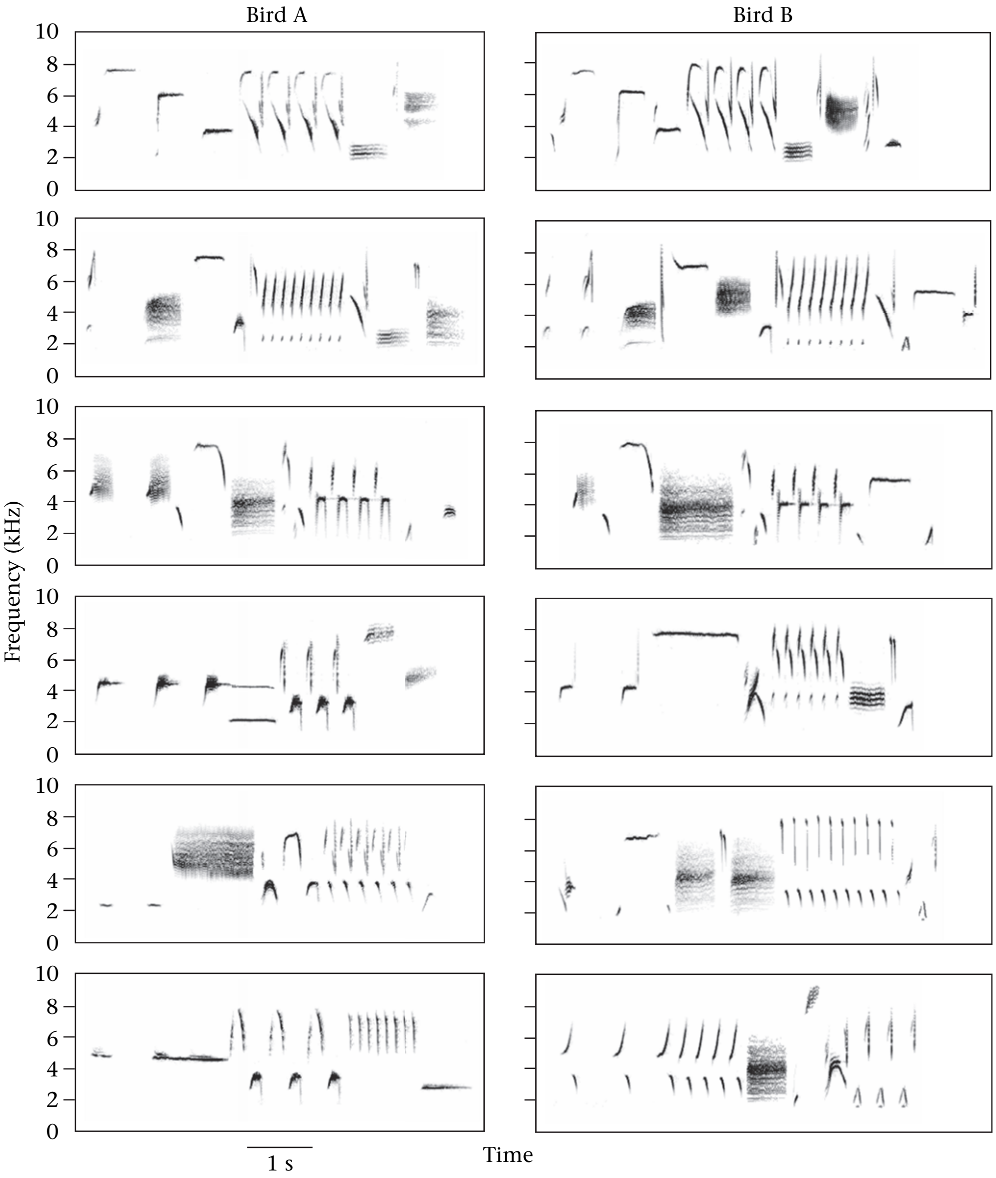

Figure 2. Song type repertoires of two song sparrow subjects. Birds A and B were neighbours and shared the first three songs in their nine-song repertoires (33% sharing). The shared songs of birds A and B are shown in the top three rows, and six of their remaining unshared types are shown in the bottom three rows.

songs for the duration of the trial. The trial was aborted if the neighbour either sang a song or approached during the trial period.

Our response measure was the subject's latency to respond (i.e. to sing or fly towards the speaker, whichever occurred first), which we predicted would be shorter in the shared song trials. We also measured the bird's closest response to the speaker, a measure of aggressive response, but our hypothesis makes no predictions concerning a difference between aggressive response to shared and unshared neighbour songs.

Experiment 2 (interactive)

In this experiment, the song playback simulated a neighbour replying to the singing subject from within the neighbour's territory. A trial began when the subject was singing and the neighbour was quiet and well away from the playback area. When the subject sang, we first identified his song type on the computer display using Syrinx. If the subject was singing a nonshared type, we waited for him to switch to a shared type. When he was singing a shared type, we replied with the neighbour's matching type, a high-threat stimulus. All trials were initiated in this way (i.e. by a type match); this can be considered the 'probe' or 'challenge' or 'escalation' phase of the trial. We played that type with 10-s pauses between songs, until the subject began to approach, which he typically did after three to six broadcast songs. As soon as we detected his initial approach, we immediately switched to a new song, either to a different shared song (a repertoire-match) or to an unshared song: this is the experimental treatment difference. We call this the 'de-escalation' phase of the trial, and all data are taken from this part of the trial. In all cases but one (subject aymi, unshared trial) the subject continued to approach the playback speaker following the switch, which probably reflects a 'momentum' effect. The question then becomes, how close does he ultimately get to the territory boundary (the playback speaker) and how long does he stay there before leaving? We played the 'de-escalation' song six or seven times, with 10-s pauses between songs, but recorded data for a full 5 min, starting from the first playback in this phase. If the neighbour interfered within the first 1.5 min of this phase, we aborted the trial; otherwise we kept the trial and cut the companion trial at this same length. Thus, for example, if on the unshared trial the neighbour interfered at the 2-min mark, we took data from just the first 2 min of both this trial and the shared trial. This concession was necessary because the playback brought the subject close to the territory boundary and his singing often attracted his neighbour (just as our playback had attracted the subject).

As in experiment 1, shared and unshared trials were run on different days, the order counterbalanced across subjects. We took the following measurements during the 'de-escalation' phase of the trial: (1) time until the subject departed, if he did (he might still be there at 300 s); (2) his closest approach distance to the speaker; and (3) the number of threat display bouts (wing waves, or quiet song, Nice 1943). Our prediction was that the bird would depart sooner and/or respond less aggressively when we switched to an unshared song than when we switched to a shared song. To provide a single overall measure of response strength, we summed the direction of response (for or against the prediction) for each of the three individual measures. For example, if the subject came to the same favourite perch on both trials (a tie), but did not display on either trial (a tie) and departed sooner on the unshared trial, this would be scored for the hypothesis. Alternatively, if the bird did not depart within 5 min on either trial (a tie), nor display on either trial, but approached closer on the unshared trial, this would be scored against the hypothesis. Our hypothesis makes no predictions concerning the number or types of songs the subject sang in the two experimental conditions.

RESULTS

Experiment 1

All 14 subjects responded sooner to shared neighbour song than to unshared neighbour song (means 20.6 versus 68.4 s; Table 1; sign test: two-tailed $P = 0.0002$), as predicted by our hypothesis. Birds responded no more aggressively on average to shared songs than to unshared songs (closest approach means were 11.7 versus 11.4 m), also consistent with our hypothesis. Although we made no predictions concerning reply songs, birds were more likely to respond with shared songs to shared song playback than to unshared song playback: 12 of 13 replies to shared playback songs were shared songs (5 of them matching songs), whereas only 7 of 13 replies to unshared songs were shared songs. Our subjects averaged 56% shared songs, which is therefore the chance expectation for shared songs as replies.

Experiment 2

Eleven of 13 subjects responded in the predicted direction (i.e. were more likely to de-escalate when the simulated neighbour switched from type matching to an unshared song rather than a shared song; sign test: two-tailed $P = 0.006$; Table 2). One subject responded opposite the prediction and another responded equally on both trials.

Table 1. Experiment 1: latency to respond, reply song and closest approach on shared and unshared song trials

	Shared song trial			Unshared song trial			Shared–Unshared	
Subject	Latency	Reply song	Approach	Latency	Reply song	Approach	Latency	Approach
orrm	70	S	30	100	S	30	−30	0
geme	30	M	30	76	S	30	−46	0
miow	10	S	15	20	S	10	−10	5
iwmi	6	M	3	45	U	3	−39	0
oyme	19	U	25	49	S	30	−30	−5
rpmb	22	S	3	56	U	1	−34	2
omrr	34	0	1	35	S	3	−1	−2
pmry	18	S	1	206	U	5	−188	−4
aymi	9	M	1	21	S	15	−12	−14
ymoo	12	M	15	103	U	5	−91	10
rmzr	8	S	1	19	U	1	−11	0
orom	9	M	6	160	U	20	−151	−14
sltr	22	S	30	37	0	1	−15	29
abam	20	S	3	30	S	6	−10	−3

Latency = time (s) from the beginning of the trial until the subject approached the playback speaker and/or sang. Approach = closest approach to the playback speaker (m) during the 3-min trial. Approaches greater than or equal to 30 m are coded as 30 m. Reply song: M = shared and matches playback song; S = shared but nonmatching song; U = unshared song; 0 = did not sing. 'Shared–Unshared' column is the difference in latency and closest approach for the shared and unshared trials.

Table 2. Experiment 2: difference between stay time, closest approach and number of displays on shared and unshared song trials

	Shared trial–Unshared trial difference			
Subject	Stay time (s)	Approach (m)	Number of displays	Sh > unsh?
orrm	232*	0	2	+
geme	0*	0	0	0
ywbm	0	15	0	+
aoma	0*	25	0	+
miow	85	0	0	+
oyme	0	22	3	+
mibb	183*	26	0	+
gbgm	205	0	2	+
aymi	0	−5	0	−
pamo	139	0	0	+
rpmb	151	4	0	+
slot3	237	0	0	+
rzmz	15*	0	4	+

Values are differences between response measures on shared and unshared trials. Positive values indicate a response in the predicted direction (longer stay time, closer approach or more displays during the shared trial). Stay time = time from the beginning of the de-escalation phase until the subject departed or 300 s elapsed. Approach = closest approach to playback speaker during the de-escalation phase. Displays = number of bouts of wing waves or quiet song. 'Sh > unsh' column sums up the signs of the three measures: 11 positive, 1 negative, 1 tie. Sign test: two-tailed $P = 0.003$.

*Neighbour interrupted after 90 s but before subject had left; see text.

DISCUSSION

The results of our two experiments fill in some of the blanks left from our previous playback studies of singing interactions between neighbouring song sparrows (Stoddard et al. 1992; Beecher et al. 1996, 2000a; Burt et al. 2001). In particular, experiment 1 suggests that, in our population, a song sparrow would address a neighbour by singing a song that they share (as well as by singing near their border and singing in the neighbour's direction). Conversely, a bird should be less likely to perceive an unshared song from a neighbour as directed to him (compared to a shared song), even if the neighbour is singing near their border and singing in his direction. Experiment 2 suggests further that an unshared song's status as not directed towards the neighbour pre-adapts it for the role of a de-escalation signal. One might argue that a better way to de-escalate an interaction would be to stop singing and leave the area; we did not test this condition in the present experiment. However, cessation of singing is not inherently a de-escalation signal, because as we have noted in all of our previous studies (Stoddard et al. 1990, 1991; Beecher et al. 1996, 2000a; Burt et al. 2001, 2002), singing rate is not a correlate of aggressive response in our song sparrow population. In fact, a song sparrow usually stops normal singing (although he may produce the qualitatively different 'quiet song') when he is responding most aggressively (closest approach to the speaker, threat displays, etc.).

Taking the results of all our studies together, they suggest that when two neighbours share some song types and not others, they may use their shared songs to modulate their social interactions in the fashion suggested by Fig. 1. To summarize the model, the bird uses the songs he shares with a particular neighbour to engage that neighbour, who may acknowledge by repertoire matching, escalate by type matching, or break off the interaction by singing an unshared song type. Thus, if our two hypothetical neighbours share songs A, B and C but no others, bird 1 can engage bird 2 by singing any one of A, B or C (towards bird 2, since other neighbours may also share some of these). If bird 1 sings (say) A, then bird 2 can acknowledge the signal by replying with B or C (repertoire-match), can escalate by replying with A, or can de-escalate by singing one of his other types.

How general might these rules be? Clearly they apply only to species with song repertoires, which make up about three-quarters of songbird species, and perhaps also to species that vary their one typical song type (e.g. chickadees can vary the frequency of their song to match; Horn et al. 1992; Shackleton et al. 1992). Do these rules apply only to species and populations with high levels of song sharing (and only to birds in that population that share with their neighbours)? Levels of song sharing appear to vary widely between populations. For example, whereas song sharing is typical in western populations of song sparrows, it is much less so in eastern populations (Hughes et al. 1998). But even in populations with low song sharing, neighbours may still have songs that are similar, or at least that the birds regard as similar, to their neighbours' songs. This can happen in two ways. First, some species of birds prune their song repertoire in their first spring, keeping songs that are similar to those of their neighbours and dropping songs that are not (e.g. Nelson 1992). Indeed the Nelson–Marler model of song learning suggests that this is a common pattern of song learning (Nelson & Marler 1994). If that is true, demonstrations that birds in a population share no more with their neighbours than with distant birds (Hughes et al. 1998) are perplexing. Second, neighbours may also have similar songs by chance. Two neighbours will have some songs in their repertoires that are more similar than others. Long-term neighbours should come to recognize which songs these are, and they could then treat these as 'shared' songs. We have recently shown that song sparrows will song-match using songs that we would not classify as the same type but that are nevertheless similar in some general way (e.g. beginning with an accelerating trill; Burt et al. 2002). Anderson et al. (2005) have also recently shown that in eastern song sparrows, which share no more songs with neighbours than with nonneighbours, a bird will nevertheless song-match songs that are partially similar to one of his own, specifically in the initial song element. In a population of western meadowlarks, *Sturnella neglecta*, where neighbours are said not to share songs, Falls (1985) has shown that birds still recognize their neighbours and show the typical patterns of song matching. Many studies have shown song matching to stranger songs, and probably in many cases (usually not documented in the papers) the 'matching' songs are similar but would not be described as 'shared' by most investigators.

In conclusion, we note that a similar pattern of repertoire usage in neighbour song interactions has been found in the banded wren, *Thryothorus pleurostictus*, a tropical songbird with many similarities to the song sparrow (Molles & Vehrencamp 1999, 2001a). In a playback study, Molles & Vehrencamp (2001b) used an 'invading/retreating singer' design in which the simulated neighbour begins to sing from 15 m within the subject's territory and then 'retreats' to the territory boundary. In one experiment, the noninteractive playback of neighbour song either switched from shared song to unshared song ('de-escalating' treatment) or continued with shared song ('aggression-maintaining' treatment). In a second, interactive experiment, the simulated neighbour type-matched the subject in the first half of the experiment and then either repertoire-matched ('de-escalating' treatment) or continued to type-match the subject ('aggression-maintaining' treatment) in the second part of the experiment. In both experiments, subjects approached the 'retreating' playback speaker sooner in the 'aggression-maintaining' treatment.

Finally, several studies with song sparrows suggest that the possession of shared songs may be advantageous, and that some of the advantage may derive improved communication between territorial neighbours. Beecher et al. (2000b) found that first-year song sparrows that shared more of their songs with their neighbourhood group held their territories for more years than did birds who shared fewer songs. Moreover, song sharing was a better predictor of lifetime territory tenure than was repertoire size. A similar correlation of survival with song sharing but not repertoire size has been found in another western song sparrow population (Wilson et al. 2000). Moreover, Wilson & Vehrencamp (2001) have shown that neighbouring song sparrows sharing more songs are less aggressive towards one another than are neighbours sharing fewer songs.

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