



Song-type matching between neighbouring song sparrows

MICHAEL D. BEECHER, S. ELIZABETH CAMPBELL, JOHN M. BURT, CHRISTOPHER E. HILL & J. CULLY NORDBY

Animal Behavior Program, Departments of Psychology and Zoology, University of Washington

(Received 16 November 1998; initial acceptance 26 January 1999;
final acceptance 9 August 1999; MS. number: A8349)

In our study population, neighbouring song sparrows typically share two or more of their 6–10 song types. In an earlier experiment, we found that established neighbours typically reply to playback of neighbour-shared song with a different song they share with that neighbour ('repertoire matching'), rather than with the same song ('type matching') or with a nonshared song. In the present experiment, we considered the hypothesis that type matching is a threat or warning signal (Krebs et al. 1981, *Animal Behaviour*, **29**, 918–923). We tested the specific prediction that a bird is more likely to type-match early in the breeding season when territory boundaries are new and still unstable, and more likely to repertoire-match later in the season, once those boundaries have become well established. Birds were played a shared song of a new neighbour once early (April) and again late (June) in the breeding season. As predicted, early in the season birds usually type-matched the playback (73% of the trials) but late in the season they type-matched only rarely (18%); birds never replied (early or late) with a nonshared song type.

© 2000 The Association for the Study of Animal Behaviour

In most species of songbirds, an individual has several distinct song types (called a song repertoire). While the territorial defence and mate attraction functions of song have been clearly established in a variety of songbirds (for review see Catchpole & Slater 1995), in many species these functions are carried out perfectly well with a single song type. For this reason song repertoires have received intense theoretical scrutiny (Searcy & Andersson 1986; Kroodsma & Byers 1991; Catchpole & Slater 1995). On theoretical question is whether singers select particular songs for particular circumstances. According to most song repertoire theories, the different songs function primarily to provide diversity, and in this view the different songs are functionally interchangeable. However, one particular pattern of song selection has been known for some time, wherein the bird replies to a stimulus song by singing the song type in his repertoire that most resembles it. This is called 'type matching' or 'song matching' (Bremond 1968; Armstrong 1973).

According to the threat hypothesis (Krebs et al. 1981), type matching by a territorial song bird signals an increased likelihood of an attack on the singing intruder. In their original presentation, Krebs et al. (1981) made two predictions. First, song-type matching should be correlated with other aspects of intense response, that is, when type matching, the bird should approach closer to the playback speaker, respond with shorter latency and

greater vigour, and so forth. Although such a correlation was found in the original study (Krebs et al. 1981), it has not been found in two subsequent studies: on the same population of great tits, *Parus major* (Falls et al. 1982), and on western meadowlarks, *Sturna neglecta* (Falls 1985). The second prediction of Krebs et al. (1981) was that type matching should be more common between territorial neighbours when territories are first set up and territory boundaries are unstable, than later in the breeding season. They provided preliminary support for this prediction, from a post hoc examination of natural rates of song-type matching in their population: rates were highest in early January, 75%, and declined to 45% in early February (chance level is approximately the reciprocal of the repertoire size, or in this species, 33%). This result has yet to be confirmed, however, in a playback experiment.

A third potential prediction of the threat hypothesis (not explicitly made in Krebs et al. 1981) is that the songs of established neighbours should be less threatening than the songs of non-neighbours ('strangers'), and therefore should be type-matched at lower rates. That birds treat neighbour song as less threatening than stranger song, at least when played from locations at which the neighbour would normally sing, has been demonstrated in playback experiments in numerous songbird species (reviews in Stoddard et al. 1991; Stoddard 1996). Although strangers' songs that are similar enough to the subjects' songs to be called 'matches' are rare, in many populations, shared songs are mostly confined to neighbouring birds (Beecher

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

et al. 1994; Nordby et al. 1999); the prediction that stranger songs will be type-matched at a higher rate than neighbour songs has been confirmed in two species. In song sparrows, *Melospiza melodia*, and western meadow-larks, both strangers' song and self song (which may be perceived as strangers' song) elicit high rates of song-type matching, whereas a neighbour's song elicits only chance-level rates (Falls 1985; Stoddard et al. 1992). In song sparrows, this higher rate of type matching to a stranger's song occurs despite the closer resemblance, on average, of the neighbour's stimulus songs than the stranger's stimulus songs to the subject's matching song types (Stoddard et al. 1992).

We recently have been able to show why type-matching rates to neighbours' songs are so low in the song sparrow. In our study population, neighbours typically share two or three of their eight or so song types (although 0 or 100% sharing is not uncommon). Although a male song sparrow rarely type-matches playback of a male neighbour's song, he usually replies instead with another one of the song types he shares with that particular neighbour, called 'repertoire matching' (Beecher et al. 1996). Note that repertoire matching requires knowledge of the singer's repertoire; in particular, the bird must know which songs he shares with the singer.

Our observations on song matching to date have been made under conditions of relative neighbour stability, mostly of long-term neighbours well into the breeding season (Stoddard et al. 1992; Beecher et al. 1996). These conditions reflect one end of the territorial interaction continuum, where territorial disputes are of low intensity and relatively uncommon. Intense territorial disputes, in contrast, tend to occur early in the breeding season, and especially between new neighbours.

With these observations as background, we have developed a revised hypothesis which views song-type matching in the normal context of territorial interactions among neighbours. We suggest that song sparrows use their selection of song types during territorial interactions as a graded signal, as suggested by Krebs et al. (1981). Suppose that a neighbour begins an interaction near the territory boundary with a song he and the subject share. By hypothesis, the subject's strongest reply would be a type match, and a weaker (perhaps de-escalating) reply would be a repertoire match (we will not speculate here on the significance of replying with an unshared song). Our previous finding of high rates of repertoire matching and low rates of type matching between neighbours are consistent with this hypothesis, because these studies were carried out mostly with long-term neighbours, and relatively late in the breeding season. In the present paper, we test the prediction that type-matching rates should be relatively high for new territorial neighbours early in their first breeding season, and should decline to substantially lower levels later in the season. This is the second prediction of the threat hypothesis by Krebs et al. (1981). In the present study we attempted to confirm this prediction and our own field observations with data obtained under the controlled conditions of using a playback experiment.

METHODS

Study Area and Subjects

Our study site is an undeveloped 3-km² park bordering Puget Sound in Seattle, Washington. The population is sedentary (nonmigratory) and typically there are about 150 males on territories in a given year. Birds move into and out of the study population from surrounding areas. The present experiment is part of a long-term study (since 1986).

For the experiment, we selected six pairs of neighbouring males as subjects. Each male served both as a subject for trials, and as a source of stimulus songs for trials on his neighbour. Neighbours were not tested on the same day. One of the birds did not appear in either of the playback trials, hence our final sample contained 11 subjects. Earlier we recorded the full song repertoires of each subject, and each pair met the following conditions: (1) they were neighbours, that is, shared a territory boundary; (2) they shared song types; and (3) one of the males was a first-year bird, and so had held his territory for only a part of that one breeding season; the other bird in each pair had held his territory for at least two breeding seasons. The inclusion of a young bird in each pair ensured that the birds were new neighbours. The repertoire sizes of the subjects in the experiment ranged from 7 to 11 song types (mean 9.18) and the number of songs shared between pairs ranged from five to eight (mean 6.34). This is higher than the average level of sharing in our population, but was ideal for our experiment because it maximized the ability of a bird to reply with a repertoire match rather than a type match, and so provided a more sensitive assay of type-matching rates. Examples of song sharing among one of these neighbour pairs are shown in Fig. 1.

Recording and Playback Equipment

We recorded song repertoires of the subjects 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 switches (method and rationale described in Kroodsmma 1982). Songs were analysed on a Kay DSP-5500 sonograph.

Playback songs were presented using an IBM Thinkpad 750P laptop computer with 16-bit sound card, attached to an amplified speaker via a 10-m cable. Playback songs were digitized in 16 bits at a 22.5-kHz sampling rate. The computer program ('Syrinx', written by J. M. Burt) allowed us to display spectrograms of all song types in the repertoires of the subject bird and his neighbour. When a bird sang, that song type could be directly compared with the songs in the display.

During a playback trial there was the possibility that the subject's neighbour would hear and respond to the playback by approaching or singing, in which case the trial would have to be aborted. To reduce this possibility, we built a highly directional speaker that consisted of a Radio Shack midrange tweeter (frequency range

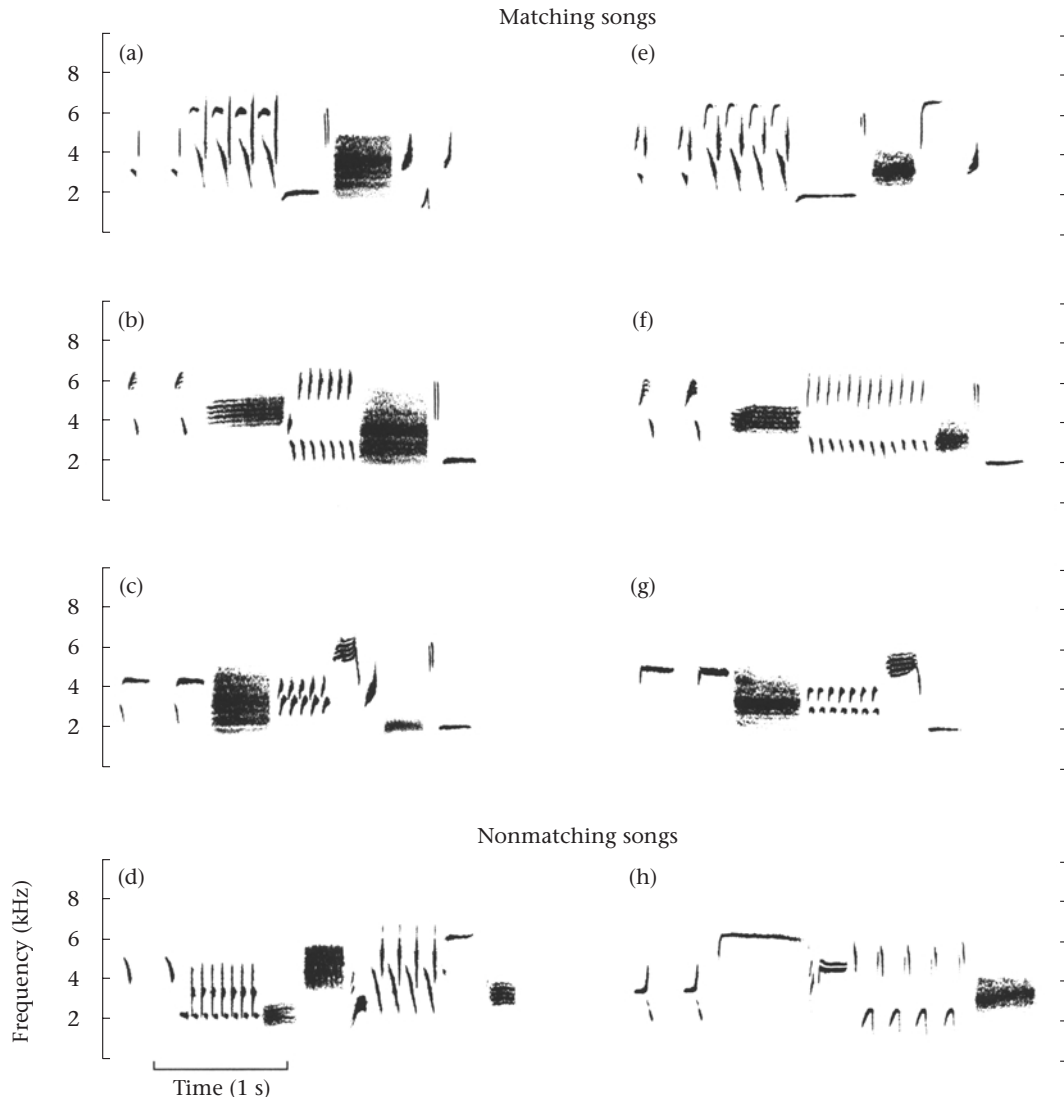


Figure 1. (a–d) Four of the 10 song types of bird IAYM. (e–h) Four of the eight song types of IAYM’s neighbour, MGAR. The top three rows show shared songs, the bottom row unshared songs. Sonagrams were made on a Kay DSP-5500 Sonagraph. Bandwidth 117 Hz.

200–20 000 Hz) attached with the speaker output at the focal point of a Sony parabolic reflector (J. M. Burt, unpublished data). The apparatus was mounted on a tripod and could be aimed at a subject bird with little or no sound heard behind it (from the neighbour’s direction).

Playback Procedure and Conditions

For each trial, we played one of the shared song types from the selected neighbour’s repertoire to the subject bird, broadcast from just within the neighbour’s side of their contiguous territorial boundary. The stimulus song was chosen randomly from those available, with the restriction that we not use a type if either bird of the pair had been singing it before the trial. For three of the 11 subjects, the stimulus song selected happened to be the same on both test days, while for the remaining eight

subjects, it was different. We did not begin a trial unless the neighbour (the stimulus bird) was out of sight and quiet. The trial was aborted if the neighbour sang or approached the playback.

The playback song was repeated every 10 s until we saw or heard the subject, at which point we began a 3-min trial. We continued playing the song at 10-s intervals until the subject sang, at which point we synchronized the playback with his singing to avoid song overlapping (playback song intervals remaining close to 10 s). If he stopped singing (no song for over 10 s) we continued our song with the 10-s intervals to the end of the 3-min trial. Post hoc comparisons revealed that playback presentation rates did not differ significantly between early and late trials nor from the rate of one per 10 s. Two trials were run for each subject, one early in the 1995 breeding season, 14–28 April, and one later, 29 May–8 June. The time between the first and second trial ranged from 31 to

Table 1. Response of 11 subjects in early- and late-season trials

Subject	Age	Repertoire size	Number shared*	Response†		Response strength‡	
				Early	Late	Early	Late
WWAM	3	8	8	TM	RM	0	3
MOBO	1	8	8	TM	RM	1	3
BRAM	3	11	6	TM	RM	4	2
OWMY	1	7	6	RM	RM	2	1
YYGM	3	9	7	RM	RM	0	2
BYMP	1	9	7	TM	RM	2	3
IAYM	3	10	5	TM	TM	0	0
MGAR	1	8	5	RM	RM	0	2
IIBM	3	10	7	TM	RM	3	1
MARG	1	11	7	TM	TM	1	1
BIMR	1	8	5	TM	RM	0	1

The neighbour of each 3-year-old is the 1-year-old immediately below him in the table.

*The number of songs shared with the bird's neighbour.

†TM: Type-match (the song matching the stimulus song); RM: repertoire-match (another shared type).

‡Response strength, 4 strongest, 0 weakest.

58 days (median 44 days). In this population the first eggs are usually laid in mid- to late March, and the last chicks fledge in early July. Border disputes between neighbours can occur at any time, but for new birds they are more common earlier rather than later in the breeding season.

The first song type the subject sang during the trial was considered his response song type. We made one exception to this rule: if the subject was singing before the trial, continued singing that same type after the onset of the trial, and subsequently switched to a new type during the trial, then the second type was counted as his response song (and the first type was subtracted in calculations of chance expectations). If the subject stayed with his pretrial song throughout the trial, that song was counted as the response song. We did this because song sparrows are bout singers, and a bird may simply continue his bout of the type he was singing when the playback began before switching to a more appropriate reply song; if the song he is already singing is an appropriate reply type, presumably he will stay with that song throughout the trial. Our exception was invoked in only two cases: on both of one subject's (BIMR) trials, the bird sang his pretrial song once or twice after playback began and then switched to a second type (which was counted as the reply type). In four other cases, a subject was singing prior to the trial, but switched to a new type as soon as he heard the first playback song. In the remaining 16 cases, the subject was not singing when we arrived.

We scored the strength of the subject's overall response on a scale of 0–4, with one point scored for each of the following: the bird (1) approached the playback speaker; (2) remained near the speaker (versus leaving the area) for the duration of the trial; (3) approached within 10 m of the speaker, and/or engaged in searching behaviour; and (4) engaged in high-intensity displays such as wing waves, high chipping, or 'quiet song' (Nice 1943).

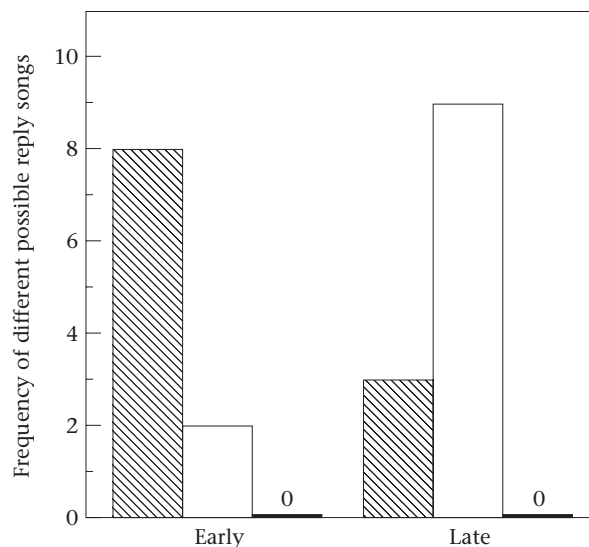


Figure 2. Frequency of different possible reply songs: type-match (▨: the song matching the stimulus song), repertoire-match (□: another shared type) or an unshared song type (■). Early: 14–28 April; Late: 29 May–8 June.

RESULTS

The results are shown in Table 1 and Fig. 2. In the early-season trials, the subjects type-matched their neighbours' stimulus songs on 73% of the trials (eight of 11 birds type-matched). In the late-season trials, the subjects type-matched their neighbours' stimulus songs on only 18% of the trials (two of 11 birds). The decrease in type matching from early to late in the season was statistically significant (Fisher's exact test: $P=0.028$). Five birds did not alter their response type from the early trial to the late trial, three displayed repertoire matching both times and two displayed type matching both times. The six birds that did switch response types, type-matched in the early-season trial and repertoire-matched in the

late-season trial, as predicted. No bird replied to their neighbour's song with an unshared song (nonmatch) on any trial.

The probability of a bird randomly responding with a type match to the stimulus song can be estimated as the reciprocal of the repertoire size (corrected as indicated in Methods), which in this sample averaged 11% (corrected median repertoire size=9). Type matching early in the season differed significantly from this chance expectation (73%, binomial test: $P < 0.0001$), but late in the season it did not (18%).

The probability of a bird randomly responding to a neighbour's song with a shared song can be estimated from the average sharing among these neighbour pairs, that is, 71%. Because of this high level of sharing, we would expect most replies to be shared songs purely by chance. Nevertheless, we obtained the most extreme response possible, that is, every bird replied to their neighbour's song with a shared type, a response which differed significantly from the chance expectation of 71% (corrected; $N=11$, $P=0.024$), or 66% if we omit the one pair of birds that shared all song types (corrected; $N=9$, $P=0.023$).

There were no observed differences in response between 1-year-old and three-year-old birds (Table 1). In particular, type-matching levels were similar in both groups: 1-year-olds type-matched on five of 12 trials, and 3-year-olds, on five of 10 trials. There was also no concordance between what neighbours of a pair did on comparable trials: they responded similarly on exactly 50% of the trials (Table 1).

We found no difference in overall response strength between early- and late-season trials (mean response early versus late=1.18 versus 1.73; $t=1.20$, $P=0.25$). We also found no difference between response strength during trials in which the bird type-matched and repertoire-matched ($N=10$ and 12, means=1.20 versus 1.67; $t=1.02$, $P=0.32$).

DISCUSSION

As predicted, birds tended to type-match early in the breeding season and repertoire-match late in the season. Our favoured interpretation of this result is that neighbour song is more threatening early in the season because of the relative instability of territory boundaries between new neighbours at that time. An alternative hypothesis is that type matching may reflect uncertainty as to the identity of the singer. A bird cannot repertoire-match another bird unless it has committed that bird's repertoire to memory. Thus, new neighbours, which are less familiar with one another early in the season than they are later in the season, would be less likely to repertoire-match. These two interpretations are not mutually exclusive, of course, but at this time we cannot distinguish between them.

Consistent with most earlier studies, we found no correlation between response strength and type matching. However, response to the playback was relatively mild in both early- and late-season trials. On only one trial (subject 'BRAM', early-season trial), did we score a response at the highest level: the bird type-matched once

before going into high-intensity (and quiet) searching behaviour near the playback speaker. The overall mild response of our birds is consistent with our observations when the neighbour song is played from the neighbour's territory. Generally, strong responses are elicited by neighbour song only when it is played from within the subject's territory, or from an inappropriate territory boundary (Stoddard et al. 1991; unpublished observations). Stranger song, on the other hand, elicits a strong response from most any location near the bird's territory.

Although in their original statement of the threat hypothesis, Krebs et al. (1981) predicted that type matching should correlate with other components of strong response, at least in the case of the song sparrow, the prediction ignores the fact that birds cease normal singing when they respond intensely to playback (or an actual intruder). Instead, the bird approaches the playback speaker, searches vigorously in the area, engages in high-intensity threat displays (wing waves), other vocalizations (high chipping, chirping, 'quiet song') or displacement behaviour (ground pecking) in the vicinity of the playback speaker (and if he finds a real intruder, he attacks him). Thus at least in this, and other similar, species it seems reasonable to amend this prediction of the threat hypothesis to say that type matching is not a component of response strength but rather a predictor or signal of the probability of a strong response in the future. An experiment to test this revised prediction would consist of two stages. The first stage would be identical to the present experiment, but once the subject bird had responded with either the same or a different song type, the threat would be escalated during stage 2, say by moving the playback speaker towards or into the subject's territory. A bird that had type-matched in stage 1 should be more likely to respond strongly to that (simulated) threat in stage 2 than a bird that had not type-matched in stage 1.

Another way of testing this modified prediction of the threat hypothesis is possible with the interactive playback technique (e.g. McGregor et al. 1992; Nielsen & Vehrencamp 1995). If the playback, which is begun when the subject is singing, is a type match, the subject should treat this as a more serious threat, and thus respond more strongly, than if it is not a type match.

How applicable are our findings to other populations of song sparrows? This question is especially pertinent given that song sharing among neighbours is reported to be minimal in some song sparrow populations. Three different eastern, migratory populations have been described as having minimal neighbour song sharing (Ontario: Kramer & Lemon 1983; Pennsylvania: Hughes et al. 1998; New York State: J. L. Bower, personal communication). These populations therefore contrast with our Washington population and two other western, sedentary populations, all of which have been observed to display high levels of song sharing (British Columbia: Cassidy 1993; California: Nielsen & Vehrencamp 1995). Although contrast suggests that the migratory-sedentary difference may be the key variable determining the extent of neighbour song sharing in the population, we have recently studied a high-elevation, migratory, Washington population that shows a high level of song sharing

among neighbours comparable to our sedentary, Washington population (Hill et al. 1999). However, even where song sharing is not as extensive as in our population, the birds themselves may classify some of their songs as 'shared' (similar to the neighbour's) or 'unshared' (dissimilar). In this case, neighbours could countersing with their 'shared' (most similar) songs and so repertoire-match and type-match just as do birds with more physically similar songs. We are presently investigating this possibility.

Although half of our subjects were first-year birds, and half 3-year-olds, we found no evidence of an age-related strategy. In particular, neither younger nor older birds were more apt to type-match than the other. It would have been interesting to test the birds earlier in the breeding season, say March, but some of the first-year birds still had variable, plastic song at this stage. We should point out that in our sedentary population, new neighbour pairs virtually always involve first-year birds, so this 'confound' cannot be removed.

Regardless of whether subsequent experiments support the modified threat hypothesis, the present study can be combined with our previous playback experiments on this population of song sparrows (Stoddard et al. 1990, 1991, 1992; Beecher et al. 1996) to draw two general conclusions. First, neighbour recognition in this population is much more sophisticated than we might have guessed. These song sparrows live in relatively stable neighbourhoods, and our playback experiments suggest that a bird not only knows his neighbour by song, but that he replies in a qualitatively different fashion to a neighbour's song from the neighbour's territory than to a stranger's song from the same place. To the neighbour's song, he replies with one of the songs he shares with the neighbour (either type matching or repertoire matching); to the stranger's song, he replies with one of the song types he does not share with that neighbour. The present study shows that these song sparrows not only preferentially use neighbour-shared songs when interacting with that neighbour, but that they select differentially within this category of neighbour-shared songs depending on the circumstances, type matching in some circumstances and repertoire matching in others.

The second general conclusion is that song similarity (song sharing) is one key dimension of communication in the countersinging context. Although in some contexts birds in this population may select their songs quasi-randomly (e.g. in the 'free' or 'advertisement' singing of unpaired birds), when interacting with neighbours, they clearly select their song types with reference to the sharing/similarity dimension. Our evidence on the importance of the sharing/similarity dimension adds to the growing evidence that birds with and without song repertoires may vary singing along a number of dimensions to modulate singing interactions with their neighbours. Other mechanisms include following versus leading versus asynchronous singing, overlapping songs, and varying the tonal frequencies of song elements (Schroeder & Wiley 1983a, b; Kramer et al. 1985; Horn & Falls 1988; Shackleton et al. 1991; McGregor et al. 1992;

Nielsen & Vehrencamp 1995; Dabelsteen & McGregor 1996).

Acknowledgments

We thank Adrian O'Loughlen, Adam Smith, Brendan Reeves, Jerry Wilkinson and two anonymous referees for comments on the manuscript, Discovery Park for hosting our field work and National Science Foundation for supporting this research. This work was presented at the ABS Annual Meeting, August 1996. The research presented here was described in Animal Research Protocol No. UW 2207-03, approved on 28 March 1996 by the Institutional Animal Care and Use Committee of the University of Washington, Seattle.

References

- Armstrong, E. A. 1973. *A Study of Bird Song*. New York: Dover.
- Beecher, M. D., Campbell, S. E. & Stoddard, P. K. 1994. Correlation of song learning and territory establishment strategies in the song sparrow. *Proceedings of the National Academy of Sciences U.S.A.*, **91**, 1450–1454.
- Beecher, M. D., Stoddard, P. K., Campbell, S. E. & Horning, C. L. 1996. Repertoire matching between neighbouring song sparrows. *Animal Behaviour*, **51**, 917–923.
- Bremond, J. C. 1968. Recherches sur la semantique et les elements vecteurs d'information dans les signaux acoustiques du rouge-gorge (*Erithacus rubecula* L.). *Terre Vie*, **2**, 109–220.
- Cassidy, A. L. E. V. 1993. Song variation and learning in island populations of song sparrows. Ph.D. thesis, University of British Columbia.
- Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: Biological Themes and Variations*. New York: Cambridge University Press.
- Dabelsteen, T. & McGregor, P. K. 1996. Dynamic acoustic communication and interactive playback. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. L. Miller), pp. 377–397. Ithaca, New York: Cornell University Press.
- Falls, J. B. 1985. Song matching in western meadowlarks. *Canadian Journal of Zoology*, **63**, 2520–2524.
- Falls, J. B., Krebs, J. R. & McGregor, P. 1982. Song-matching in the great tit: the effect of song similarity and familiarity. *Animal Behaviour*, **30**, 997–1009.
- Hill, C. E., Campbell, S. E., Nordby, J. C., Bur, J. M. & Beecher, M. D. 1999. Song sharing in two populations of song sparrows. *Behavioral Ecology and Sociobiology*, **46**, 341–349.
- Horn, A. G. & Falls, J. B. 1988. Repertoires and countersinging in western meadowlarks. *Ethology*, **77**, 337–343.
- Hughes, M., Nowicki, S., Searcy, W. A. & Peters, S. 1998. Song type sharing in song sparrows: implication for repertoire function and song learning. *Behavioral Ecology and Sociobiology*, **42**, 437–446.
- Kramer, H. G. & Lemon, R. E. 1983. Dynamics of territorial singing between neighboring song sparrows (*Melospiza melodia*). *Behaviour*, **85**, 198–223.
- Kramer, H. G., Lemon, R. E. & Morris, M. J. 1985. Song switching and agonistic stimulation in the song sparrow (*Melospiza melodia*): five tests. *Animal Behaviour*, **33**, 135–149.
- Krebs, J. R., Ashcroft, R. & van Orsdol, K. 1981. Song matching in the great tit *Parus major* L. *Animal Behaviour*, **29**, 918–923.
- Kroodsma, D. E. 1982. Song repertoires: problems in their definition and use. In: *Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 125–146. New York: Academic Press.

- Kroodsma, D. E. & Byers, B. E.** 1991. The function(s) of bird song. *American Zoologist*, **31**, 318–328.
- McGregor, P. K., Dabelsteen, T., Shepherd, M. & Pedersen, S. B.** 1992. The signal value of matched singing in great tits: evidence from interactive playback experiments. *Animal Behaviour*, **43**, 987–998.
- Nice, M. M.** 1943. Studies in the life history of the song sparrow II. The behavior of the song sparrow and other passerines. *Transactions of the Linnean Society of New York*, **6**, 1–328.
- Nielsen, B. M. B. & Vehrencamp, S. L.** 1995. Responses of song sparrows to song-type matching via interactive playback. *Behavioral Ecology and Sociobiology*, **37**, 109–117.
- Nordby, J. C., Campbell, S. E. & Beecher, M. D.** 1999. Ecological correlates of song learning in song sparrows. *Behavioral Ecology*, **10**, 287–297.
- Schroeder, D. J. & Wiley, R. H.** 1983a. Communication with repertoires of song themes in tufted titmice. *Animal Behaviour*, **31**, 1128–1138.
- Schroeder, D. J. & Wiley, R. H.** 1983b. Communication with shared song themes in tufted titmice. *Auk*, **100**, 414–424.
- Searcy, W. A. & Andersson, M.** 1986. Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, **17**, 507–533.
- Shackleton, S. A., Ratcliffe, L., Horn, A. G. & Naugler, C. T.** 1991. Song repertoires of Harris' sparrows (*Zonotrichia querula*). *Canadian Journal of Zoology*, **69**, 1867–1874.
- Stoddard, P. K.** 1996. Vocal recognition of territorial passerines. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. L. Miller), pp. 356–374. Ithaca, New York: Cornell University Press.
- Stoddard, P. K., Beecher, M. D., Horning, C. H. & Willis, M. S.** 1990. Strong neighbor-stranger discrimination in song sparrows. *Condor*, **97**, 1051–1056.
- Stoddard, P. K., Beecher, M. D., Horning, C. L. & Campbell, S. E.** 1991. Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. *Behavioral Ecology and Sociobiology*, **29**, 211–215.
- Stoddard, P. K., Beecher, M. D., Campbell, S. E. & Horning, C.** 1992. Song-type matching in the song sparrow. *Canadian Journal of Zoology*, **70**, 1440–1444.