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# A test of the deceptive mimicry hypothesis in song-sharing song sparrows

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Deceptive mimicry is one of several hypotheses for the evolution of song copying in oscine songbirds. This hypothesis predicts that a floater or immigrant male that sings local song types may be perceived as a territory owner and benefit from the reduced aggression commonly observed between established neighbours ('dear enemy' effect). The present study employed a field playback experiment to test the short-term ability of mimics to deceive territorial male song sparrows, *Melospiza melodia*. A set of three nonshared song type stimuli was presented to individual focal birds from the territory boundary of an adjacent male: a song type recorded from this adjacent neighbour (Neighbour), and two from nonneighbouring males that were an unfamiliar song type (Stranger) and a song type in the neighbour's repertoire (Mimic). The behavioural response to the Mimic was often as strong as, and sometimes stronger than, the response to the Stranger and was significantly more aggressive than to the Neighbour. Thus most birds accurately assessed the Mimic as a non-neighbouring invader. This study also revealed a significant negative correlation between the number of songs a subject shared with his neighbour and his aggressive response to the Neighbour stimulus. Song sharing is associated with reduced aggression between neighbours, but the mechanism is not deceptive mimicry. In this species with age-restricted learning, song sharing may serve as an indicator of a bird's competitive strength and ability to establish and maintain a territory near his adult song tutors.

In territorial systems where established neighbours are a lesser threat than non-neighbours, neighbouring territory owners can avoid costly and unnecessary fighting by recognizing and responding less aggressively to one another's signals. This phenomenon is referred to as the 'dear enemy' effect (reviewed by Temeles 1994). Rohwer's (1982) theory of deceptive mimicry predicts that floatermales might capitalize on this reduced aggressive tendency by mimicking the signals (songs) of resident birds. Such mimicry could facilitate territory establishment by floaters via deception of existing territory owners and other competitors as to a bird's true residence status. Deceptive mimicry is one of several hypotheses for the adaptive significance of whole song copying in oscine songbirds (Payne 1983).

For deceptive mimicry to operate, learning males must be selected to copy songs extremely accurately from resident tutor males, and receivers must be prone to at least occasional recognition errors. Neighbour

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recognition was believed to be more difficult in repertoire species because of the large number of song variants receivers must learn for each neighbour (reviewed by Stoddard 1996). Although numerous discrimination studies have since provided good evidence for accurate neighbour-stranger discrimination in repertoire species, McGregor & Avery (1986) and McGregor (1988) showed that great tits, Parus major, displayed poor recognition of new neighbours if the replacement neighbour sang song types of prior neighbours. Similarly, in a study that tested the memory constraints on the number of different song types a bird could learn to distinguish, male song sparrows, Melospiza melodia, initially confused matching song types from different birds (Stoddard et al. 1992a). Laboratory studies designed to unravel the basis of recognition and discrimination of neighbours from strangers have produced equivocal results. Weary & Krebs (1992) suggested that great tits could recognize the songs of individual males, even if they had not heard the specific song types before, based on general voice characteristics of song types to which they had been exposed. However, the sample size of this study was small and the presence of extraneous cues was not excluded (Lambrechts & Dhondt 1994). A similar study on song sparrows found that receivers classify newly heard songs by song type rather than by singer identity (Beecher et al. 1994a). That study raised the possibility that neighbour recognition in repertoire species is based on repertoire composition rather than voice characteristics or individual signature variants of each song type.

Several correlative field studies have explicitly examined the deceptive mimicry hypothesis. In indigo buntings, Passerina cyanea, a species with one song type per male, yearlings that copied and matched the song type of an adult neighbour were more successful in pairing, fledging offspring and maintaining territory occupancy than males that did not match (Payne 1982). In extensive tests of four alternative hypotheses for song copying, the strongest support was obtained for there being an advantage in ongoing competitive male interactions, specifically in territory defence. Song-copying males occurred in higher-quality habitats, countersang more aggressively with their neighbours, and were more effective in preventing both floaters and neighbours from intruding into their territories (Payne 1983; Payne et al. 1988). In addition, there was no evidence that replacement territorial males copied the song of the prior owner, a key prediction of the deceptive mimicry hypothesis. McGregor & Krebs (1984) also found no tendency for replacement male great tits to share more song types with the prior owner, but they did find that birds with larger repertoires shared more song types with neighbours and had higher reproductive success than males with smaller repertoires and lower sharing. Thus field observations do not support the deceptive mimicry hypothesis for song copying and tend to support alternative hypotheses.

In the study reported here, we designed a field playback experiment that provides a stronger test of the deceptive mimicry hypothesis. Our subjects were territorial male song sparrows from a nonmigratory southern California subspecies (*M. m. cooperi*). Song type sharing ranges from 0 to 86% (mean of 22%, average repertoire size=9.6), and males sharing an average of two or more song types with their adjacent neighbours were shown to have a significantly higher probability of maintaining territory ownership than males sharing few or no song types (Wilson et al. 2000). We quantified the behavioural responses of focal birds to the playback of a nonshared song type that closely matched a song type from an adjacent neighbour's song repertoire but was recorded from an unfamiliar, non-neighbouring bird (i.e. a mimic). In order to interpret the strength of the aggressive response to the mimic, we also stimulated each focal bird from the same territory boundary location with two other playback treatments: a song of the same type as in the mimic treatment but recorded from the true neighbour, and a song from an unfamiliar bird that was unlike any song type from either the focal bird or the neighbour. These two latter treatments are equivalent to the stimuli typically used in neighbour-stranger discrimination experiments. Our protocol therefore could be called a neighbour-mimic-stranger discrimination experiment.

Song sparrows are known to display milder aggressive approach responses to neighbour playback than to stranger playback (Harris & Lemon 1976; Kroodsma 1976; Searcy et al. 1981; Stoddard et al. 1990, 1991), and this provided us with a means to evaluate whether the subjects classified our mimic stimuli as familiar neighbours or unfamiliar non-neighbours. If the focal bird responded to the mimic in the same way that he responded to the neighbour, it would suggest that he had misidentified the mimic as the neighbour and was using only song type and location to identify his neighbour, a strategy vulnerable to deceptive mimicry. If the response to the mimic playback was similar to that of the stranger playback, then he was not deceived by the mimic and was using either voice characteristics or fine details of the song type to discriminate the neighbour from the stranger. An aggressive response that was intermediate to the responses to the neighbour and stranger playbacks could indicate some level of confusion or the need to listen to more renditions of the stimulus before mounting an aggressive approach. A response to the mimic that was stronger than the response to the stranger implies that a stranger singing local song types is perceived as a greater threat than a stranger singing unfamiliar song types.

## METHODS

The playback experiment was conducted from April to June 1998, in an urban park area surrounding a natural fresh water marsh system (Kit Carson Park, Escondido, California, U.S.A.). The habitat consisted of connected ponds edged with cattails (Typhaceae), willows (*Salix* spp.) and gum trees (*Eucalyptus globulus*). One side of the study area was contiguous with a large, densely vegetated marsh containing a high density of song sparrows, whereas the other sides were surrounded by either mowed grass or *Eucalyptus* forest. Song sparrows nested, sang and defended territories in the rim of vegetation around the ponds, but often foraged in the surrounding habitat. Banding and recording of the sparrows began in 1997, so we knew the histories of some of the birds present in 1998.

We compared the responses of 12 male song sparrows to Neighbour, Stranger and Mimic stimulus trials. All subjects were individually colour-banded. The Neighbour stimulus was a song type recorded from an adjacent neighbour that was not shared with the focal bird. By using a song type absent from the focal bird's repertoire, we prevented him from directly song-type matching the playback. This restriction also eliminated any heightened discrimination ability the bird might have had with a song type in his own repertoire. The Stranger stimulus was a song type present in neither the repertoire of the focal bird nor the neighbour and was recorded from a non-neighbouring male in the population. The Mimic stimulus was a song type present in the neighbour's repertoire that was recorded from a non-neighbouring male. With the exception of two playback sets, the Mimic song type was the same as the one used in the Neighbour trial. All songs were recorded with a Teac DA-P20 digital recorder and Sennheiser MKH816 directional microphone. Digitized songs were filtered and amplified, if necessary, using Canary sound analysis software (Charif et al. 1995). Low-frequency road noise was filtered from

all stimuli and selective amplification ensured consistent broadcast volume in the field (see below). To control for unanticipated differences in sound quality, many songs had roles as Neighbour, Mimic and Stranger songs in playbacks to different males. We used a total of 41 songs for the experiments.

We exposed each experimental male to all three treatments from the same location on the territory boundary between the focal bird and the neighbour whose song was given in the Neighbour trial. We presented the three treatments in random order on separate mornings between 0700 and 1000 hours. Two investigators were always present: one selected and presented the playback stimuli, while the other observed and announced the focal bird's responses without any knowledge of the playback treatment type. Experiments were run interactively using Singit! (Bradbury & Vehrencamp 1994) on a Macintosh PowerBook 1400c to avoid overlapping the focal bird's songs. The computer was connected via an 8-m cable to an amplified Bose Roommate II speaker on a tripod. A sound-absorbent, rubber-coated recording parabola was mounted behind the speaker so that sound directed into the neighbour's territory was either absorbed or reflected forward (adapted from a design by J. Burt: http://www.syrinxpc.com/speaker.html). Peak amplitude of all stimulus songs measured in the park during morning hours was between 69 and 72 dB at 8 m in front of the speaker, the same amplitude as males used in the experiments (these measurements include ambient noise in and around the park). At the same distance behind the speaker, no signal was detected beyond ambient noise. The speaker was placed on the territory boundary or 1 m within the focal bird's territory to avoid neighbour interference. Preliminary trials showed that playback from within the neighbour's territory elicited neighbour interference and retreat of the focal bird. Boundaries shifted throughout the season and were monitored 1-3 days before and immediately prior to playback by observing territorial disputes and countersinging.

Playback began only after we located both the neighbour and the focal bird and both were silent for at least a minute. We delivered approximately 18 songs of the same type at 10-s intervals for 3 min; we extended song separation by 1-3 s if the focal bird was singing at 10 s from the last playback. We monitored postplayback responses for an additional 3 min. We tape-recorded all trials for subsequent analysis of singing responses. We quantified other behavioural responses, including latency to sing or approach, approach distances (2, 5, 10, 15, or 20+m) to the speaker and flights of 1 m or more, with the event recorder in Singit! and announced these on the tape recordings. We presented 24 complete Neighbour-Mimic-Stranger playback sets to the 12 focal males from territory boundaries with different neighbours. Four males heard one playback set and the remaining eight males were exposed to two to four playback sets, each from a different territorial boundary. Song stimuli were different for each boundary. Playback sets to the same male from different boundaries were separated by at least 5 days to avoid excessive stimulation, with the exception

of four sets that were initiated 1–3 days after the previous set. We also maximized the distance between males tested on the same day and found no time of day or presentation order effects in any of the response variables (analyses of variance, ANOVA: all NS). We controlled for individual male differences in our analyses (see below).

The similarity of the Mimic song to the Neighbour's song of the same type was quantified using visual comparison of spectrograms. Two judges examined each pair of spectrograms and ranked their similarity on a scale of 1 (poor match) to 4 (excellent match). We placed more importance on the frequency, note shape and note order of the first half of the songs, since the second half of the song varies considerably within birds and song sparrows themselves place more importance on the introductory notes (Horning et al. 1993). Judges agreed on similarity ranking in 22 of 24 cases (92% concordance). When judges disagreed, the lower of the two similarity rankings was used. We used three 1s, nine 2s, four 3s and eight 4s. Figure 1 shows an example of each song similarity rank.

Because many of the behavioural response measures were correlated with each other, we used multivariate techniques to reduce the number of variables to a smaller set of orthogonal composite score variables. Instead of the popular principal component (PCA) and factor analyses, which seek to partition only the overall variance in the response variables into a set of components or factors with decreasing variance, we used multiway analysis of variance (MANOVA: Hopp & Morton 1998). MANOVA extracts a set of canonical variates among the response variables that maximally separates the groups or treatments of interest. When there are three or more groups, the first canonical variate is the one that maximally separates the most separable groups, the second variate separates groups maximally but independently of the first, and so on. The weightings of the original variables in the canonical variate scores reveal the relative ability of the variables to explain the group differences. The overall significance of a MANOVA is therefore likely to be much greater than a PCA followed by ANOVA. However, because MANOVA by definition maximizes group differentiation, hypothesis testing must be limited to subsets of the groups. In our case, we were interested in whether the Mimic was treated more like the Neighbour or the Stranger, so our post hoc tests separately examined only the Mimic-Stranger and Mimic-Neighbour differences. Focal bird identity was included as a second (random) factor to control for individual response differences. Our analysis was thus a two-way MANOVA with main factors playback treatment and bird, plus the treatment\*bird interaction. We used the general linear modelling (GLM) platform of JMP 3.2 (SAS Institute 1997) to run the analyses. As with any multivariate technique, variables are assumed to be multivariate normal. We transformed skewed variables (natural log or square root) to visually approximate a normal distribution, but several variables were platykurtotic or bimodal and could not be transformed. This type of deviation leads to an overestimate of the error variance and therefore has a conservative effect on the interpretation of significance (Tabachnick & Fidell 1996). Variables were standardized so that canonical



Figure 1. Examples of shared song types from different individual birds at each of our ranks of visual similarity. The first half of the song is weighted more strongly than the ending. Rank 1 is the lowest similarity score, Rank 4 is the highest.

variate weightings of the individual variables could be more easily compared.

We treated the playback sets to the same focal male from different boundaries as independent experiments because the responses of focal birds to their neighbours differed depending on the number of song types shared with each neighbour. For the seven focal males that shared different numbers of song types with their neighbours, we compared the aggressive response (canonical variate 1) towards the neighbour with the highest sharing level to the aggressive response towards the neighbour with the lowest sharing level. Responses to the Neighbour playback treatment were significantly stronger to the neighbour with the lower sharing level (Wilcoxon matched-pairs signed-ranks test: T=26, N=7, two-tailed P=0.046), but responses to the Mimic and Stranger treatment did not depend on sharing level (NS). Because the response to the Mimic relative to the responses to the Neighbour and Stranger was the key test in our experiment, we could not average the treatment values for the neighbours of a given focal male.

All other statistical analyses were computed with StatView 5.0 (SAS Institute 1998). Parametric tests were used when variables were normally distributed or easily transformed to be normal. We used the nonparametric

Friedman two-way ANOVA in univariate analyses of severely non-normally distributed variables because of its ability to control for bird effects. Means reported in the text include  $\pm$  standard deviations.

### RESULTS

Table 1 shows the mean values of each of the response variables for each playback treatment. Univariate nonparametric analyses indicated that male song sparrows responded significantly differently to the Neighbour, Mimic and Stranger treatments in terms of two key aggressive approach variables: closest approach to the speaker and time spent less than 5 m from the speaker in the postplayback period. These two response variables were also found to differ between treatments in other studies of song sparrows, whereas singing behaviour during the playback period typically did not differ (Harris & Lemon 1976; Kroodsma 1976; McArthur 1986; Stoddard et al. 1988, 1990).

The MANOVA yielded a highly significant overall model, with significant effects of both the treatment and bird main effects but no significant interaction term (Table 2). Figure 2 shows the treatment centroid plot of the first two canonical variates. The first variate strongly

Response variable	Neighbour	Mimic	Stranger	$\chi^2_2$	Р
Closest approach (m)	6.4±6.6	4.5±6.7	2.9±2.3	11.24	0.004
Time $<5$ m during (s)	85±80	116±62	134±55	2.79	0.248
Time $<5$ m after (s)	96±84	142±66	147±65	9.10	0.011
Latency to respond (s)	59±85	26±28	23±18	1.00	0.607
Songs during	9.5±7.6	9.6±5.5	12.1±6.0	5.83	0.054
Songs after	5.2±4.7	8.2±6.8	8.4±6.3	3.58	0.167
Flights during	7.9±6.8	10.5±6.9	11.1±7.2	3.06	0.217
Flights after	4.5±4.0	4.4±3.0	5.3±3.9	0.36	0.834

Table 1. Mean±SD and statistical difference of response variables for Neighbour, Mimic and Stranger song stimuli\*

\*Statistical test results based on nonparametric Friedman two-way ANOVA. N=24 for each treatment. Only closest approach remained significant with a Bonferroni correction, where  $P_{crit}=0.006$ .

Table 2. Results of MANOVA tests

Test	Factor	F	df	Р
Whole model	Bird	3.034	88,200	<0.0001
	Bird×treatment	1.206	176,234	0.090
Mimic–Neighbour contrast		5.029	8,29	0.0006
Mimic–Stranger contrast		1.192	8,29	0.338



**Figure 2.** Centroid plot of the three treatments using the first versus the second canonical variates. The 95% confidence circles are shown. Nonoverlapping circles generally indicate a significant difference. Higher values of both canonical variates are associated with a stronger aggressive response.

weighted with closest approach, latency to respond with either song or approach, time within 5 m of the speaker during and after playback and flights during playback, and best separated the Neighbour and Mimic treatments. The second variate weighted with song rate during and after playback and added only a small additional amount of separation between the Mimic and Stranger treatments. In the post hoc tests of the Mimic treatment versus each of the other treatments, the response towards the Mimic did not differ significantly from the response to the Stranger but did differ significantly from the response to the Neighbour. Thus, the Mimic was treated aggressively, more like a Stranger than a Neighbour.

There was considerable variation in the relative responses to the three treatments among focal birds. Figure 3 compares the first canonical variate scores for Neighbour, Mimic and Stranger playbacks to each subject. Playback sets were classified as 'correct', 'incorrect' or 'ambiguous' according to the response to the Mimic relative to the Neighbour and Stranger (classifications are shown in the figure). Overall, the response to the Mimic was highly aggressive, stronger than the Neighbour response in 19 of the 24 playback sets, and stronger than the Stranger response in 11 sets. The Mimic was considered correctly identified as a non-neighbour in 16 of these cases because the response to the Mimic was either more aggressive than both Neighbour and Stranger, or more similar to the Stranger than to the Neighbour. In four sets, the Mimic was closer to the Neighbour than to the stranger, and in another two cases the Mimic was lower than the Neighbour, making a total of six playback sets that were classified as incorrect. In two of the sets, the difference in response to all three treatments was negligible, so these cases were considered ambiguous. Interestingly, in 10 of the sets, the response to the Neighbour was similar to or more aggressive than the response to the Stranger, implying that only 14 cases showed the expected 'dear enemy' pattern.

We examined the degree to which the responses of the birds depended on how closely the Mimic song matched the neighbour's song. One would expect misidentification to be more likely when songs are more similar. Contrary to expectation, there was no significant difference in the mean visual song similarity ranks for



#### Playback set

**Figure 3.** Aggressive responses to each playback treatment split by playback set. The vertical axis is the first canonical variate of the MANOVA. The subject and his respective neighbour are indicated on the horizontal axis, and responses have been classified as C (correct identification of the Mimic as a non-neighbour), I (incorrect response to the Mimic, which suggests misidentification) and A (ambiguous response to the Mimic, which can be classified as neither correct nor incorrect).

correct (2.50) versus incorrect (2.83) sets (unpaired *t* test:  $t_{20}$ =0.652, *P*=0.522). The aggressive score towards the Mimic for all 24 sets was also unrelated to Mimic–Neighbour song similarity (regression: *r*= - 0.303,  $F_{1,22}$ =2.23, *P*=0.150).

Most of the sets in which focal birds responded aggressively to all treatment types occurred at highly contested, unstable boundaries where the two neighbours were frequently observed to engage in chasing, lunging, boundary-walking, soft singing and wing-waving throughout the breeding season. These contested boundaries primarily involved three individual birds (BW, BY and GY) with their two adjacent neighbours. Note in Fig. 3, where the sets are ordered from left to right according to increasing aggressive score towards the neighbour, that the sets involving these three birds primarily occur on the right. These three birds responded extremely aggressively to the playback of their neighbours' songs (first canonical variate= $0.212 \pm 0.151$ ), and the neighbours in turn were moderately aggressive when stimulated with BW, BY, or GY song playback  $(-0.169 \pm 0.245)$  and less aggressive towards other neighbours  $(-0.359 \pm 0.377)$  (ANOVA:  $F_{2,21}=7.000$ , P=0.005). All three of these males subsequently disappeared from the study area. We reran the MANOVA omitting all sets in which these three birds were focals, but found no differences in the centroid plot appearance or the significance of the post hoc tests.

We noticed that BW and BY shared no song types with either of their neighbours, while GY shared 1.5 and 3.0 song types with his neighbours. We therefore asked whether there was a general association between neigh-



**Figure 4.** Regression analysis of the aggressive response (first canonical variate) of subjects to the Neighbour stimulus versus the number of song types shared with the neighbour. Results were similar when other aggressive approach response variables were used as the dependent variable (time spent less than 5 m from the speaker, closest approach).

bour aggression and degree of song sharing. A significant negative correlation was found between the number of songs shared between two neighbouring birds and their aggressive response (first canonical variate) during the Neighbour treatment trials (regression: r = -0.446,  $F_{1,22} = 5.46$ , P = 0.029; Fig. 4). In particular, subjects sharing more songs with the neighbour spent less time close to the speaker and did not approach as closely (regressions: r = 0.520 and 0.450,  $F_{1,22} = 8.15$  and 5.59, P = 0.009 and 0.027, respectively). No significant relationships were

found between song-sharing level and any of the aggression measures for the Mimic and Stranger treatments. Song-sharing neighbours thus treat each other with greater reserve than nonsharing neighbours.

# DISCUSSION

The majority of our subjects treated the Mimic playback stimulus aggressively, as they would an unfamiliar intruder. We therefore conclude that they quickly identified the Mimic correctly as a non-neighbouring bird even though the stimulus song matched a song type in the neighbour's repertoire. However, males in six of the 24 playback sets may have been deceived, since they responded to the Mimic with mild aggression as they would a neighbour at a stable boundary. The likelihood of misidentifying the Mimic was not related to the degree of similarity to the neighbour's song, although our visual ranking method of song similarity may not have captured the most important features of song classification used by the birds. We do not believe that these few cases of deception provide strong support for the deceptive mimicry hypothesis for song copying in western populations of the song sparrow. Our experimental design only addresses the possibility of short-term misidentification of the singer's identity. In operant conditioning experiments, Stoddard et al. (1992a) found that song sparrows were initially confused by shared song types by different singers, but could successfully discriminate between the songs given additional time to learn. Moreover, normal contests for territories or boundary positions occur over a series of repeated encounters and birds would be expected to switch among song types several times (Arcese 1987; Bower 2000). Since birds generally share only a few song types with other birds, an invading mimic eventually would sing a song type not present in the repertoire of its model and expose itself as an impostor.

These results bear on the issue of what specific cues receivers might learn and use to distinguish among individual neighbours, in addition to their location. Three cues have been suggested: (1) the composition of the song type repertoire, (2) unique voice characteristics common to all song types of a given individual, or (3) minor differences in the song type versions of each territorial neighbour. Repertoire composition and/or song type sequence ought to be a more useful cue for immediate variety singers (Verner 1976; Todt et al. 1979; Brindley 1991) than for bout singers such as song sparrows because a larger sampling of the repertoire is given per unit time. In a neighbour-mimic-stranger experiment performed on banded wrens, Thryothorus pleurostictus, an immediate variety singer with a larger repertoire size, higher sharing level and greater song similarity than the song sparrow, the birds confused the mimic with the neighbour in 50% of cases (Molles & Vehrencamp 2001). The 27% confusion rate in the current study suggests that song sparrows may rely on repertoire composition only to a small degree. Individually distinctive voice characteristics can be generated by unique resonating and filtering mechanisms, variations in syringeal and bill morphology,

body-size related frequency differences, or small variations in amplitude and frequency modulations (Nowicki 1987; Williams et al. 1989; Weary et al. 1990; Suthers 1994; Baptista 1996; Fee et al. 1998). Although great tits, with their smaller repertoires and simpler song structure, may be able to use voice characteristics alone to correctly classify singer identity (Weary & Krebs 1992), song sparrows could not classify with this cue (Beecher et al. 1994a). The most important recognition mechanism for song sparrows seems to be memorization of subtle differences in song type variation among adjacent neighbours. Biased song copying can easily generate slight, consistent differences in renditions of song types (Verner 1976; Kroodsma 1982; Schroeder & Wiley 1983; Weary et al. 1990). Podos et al. (1992) showed that within-type song variation in song sparrows was lower within birds than between birds, allowing for the real possibility that birds rely on individual variants of song types in the field. Song sparrows have been shown to be sensitive to within-type song variation and have the memory capacity to learn over 60 different songs (Stoddard et al. 1988, 1992a). Our study showed that most birds could quickly distinguish a neighbour mimic from the true neighbour, providing strong support for a primary reliance on individual song type variants as cues for individual recognition.

In lieu of deceptive mimicry, alternative hypotheses must be sought for the evolution of song copying. There is now abundant evidence that western subspecies of song sparrows use shared and matching song types in strategic ways to point to specific rivals and neighbours and to indicate short-term aggressive versus nonaggressive intentions (Beecher et al. 1996, 2000a; Burt et al. 2001; Vehrencamp 2001). Song sparrows also respond differently to matching, shared and nonshared song types (McArthur 1986; Stoddard et al. 1992b; Nielsen & Vehrencamp 1995; Burt et al. 2001; Vehrencamp, 2001). We explicitly held this short-term source of variation constant in our study by using only stimulus song types that were not present in the focal birds' repertoires, which prevented them from type matching. Nevertheless, nonsharing neighbours in the long term lack the vocabulary to deliver escalating versus de-escalating signals, so conflicts may be more frequent because all songs are considered threatening.

The poor ability of nonsong-type-sharing birds to establish a dear enemy relationship with their neighbours suggests another hypothesis for song copying besides deception or strategic signalling. Stoddard et al. (1991) also found weaker neighbour-stranger discrimination at unstable territorial boundaries because all responses were strong, but they did not relate this occurrence to levels of song sharing. Our discovery was a fortuitous outcome of conducting playback sets in both directions at every boundary between males in the study area. The highly aggressive behaviour of nonsharers towards their neighbours, and the strong reciprocal aggression of the neighbours towards them, is undoubtedly the proximate mechanism for the low survival of nonsharers (43%) relative to sharers (82%) (Beecher et al. 2000b; Wilson et al. 2000). We also observed that new (presumably yearling) birds with higher song sharing were able to squeeze into small unoccupied spaces and subsequently enlarge their territories to the normal size by the next year, whereas new birds with low or no song sharing were unable to enlarge their territories and disappeared. One of our beleaguered birds (GY) was an older individual who shared a few songs with his neighbours but appeared to weaken during the second study year; he was perpetually harassed by a young song sharer (GG) who eventually took over the territory. Prior playback studies have shown that territory owners respond more aggressively to strangers singing songs shared with the focal bird than to strangers singing unfamiliar songs (Nielsen & Vehrencamp 1995), and in the current study even strangers mimicking neighbours evoked stronger responses, suggesting that invaders singing local song types are perceived as greater threats. All of this evidence leads to the conclusion that the level of song sharing with neighbours (number of shared song types and perhaps even song type similarity) is associated with a bird's competitive ability.

A link between song sharing and competitive ability could be generated in several ways. If song learning in young birds is restricted to the predispersal period, and competition is strong for territories in the natal or tutor home range area, then only good competitors will win territories close to their tutors with which they share songs, and poor competitors will be forced to disperse farther where they share fewer songs. This idea is supported by studies of dominance and territory acquisition by Arcese (1987, 1989a, b; Arcese & Smith 1985) and song learning and dispersal by Beecher et al. (1994b) and Nordby et al. (1999). Song learning is restricted to the first few months of life in this species (Marler & Peters 1987) but may extend up to 6 months of age in the western subspecies (Nordby et al. 2000). In this scenario, the number of song types a male shares with his neighbours is an inverse index of the distance he has dispersed from his song-learning area, and better competitors disperse shorter distances, so song sharing becomes an indicator of competitive ability. Another possible mechanism that could generate the sharing/competitive ability link is a quality- or condition-dependent constraint on song memorization or learning duration, such that higherquality birds can memorize more song types or extend the period of learning until after dispersal (Nowicki et al. 1998, 2000). Regardless of the mechanism that generates the link between sharing and competitive ability, weaker (nonsharing) birds are constantly harassed by their stronger neighbours and forced to defend their territories vigorously, whereas stronger (song-sharing) birds establish stable boundaries with their equally strong neighbours.

In conclusion, song copying and song type sharing in an age-restricted learner such as the song sparrow is more likely to have evolved as an honest indicator signal of a male's local origin, quality and/or fighting ability, rather than as a deceptive signal of a male's residence status. This relationship will not be true in species with open-ended learning and in migratory populations where competition to acquire territories close to the natal home range is absent (Vehrencamp 2000).

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