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ARTICLES

Mate, neighbour and stranger songs: a female song sparrow perspective

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We investigated discrimination by female song sparrows, *Melospiza melodia*, between different categories of male song using the copulation solicitation display as a preference assay. Females responded most strongly to songs recorded from their mates, less strongly to songs of neighbouring males and least strongly to songs of stranger males. Among the stranger songs, however, females preferred songs that were most similar structurally to song types in their mates' repertoires (matching songs). These results are interpreted as evidence that females can recognize individual males based on the songs in their repertoires. Moreover, the observed female preferences for nonmatching neighbour and matching stranger song over nonmatching stranger song, suggest that any male with songs structurally similar to mate songs or even to nonmate but local neighbourhood songs, will be at an advantage in sexual interactions with local females.

Individual recognition based on song has been demonstrated in the majority of territorial songbird species investigated to date (Falls 1982; Stoddard 1996). Studies have focused on the ability of males to discriminate between neighbour and stranger males, and, to a lesser extent, to distinguish between different neighbouring males. Evidence of recognition has been found in both of these circumstances. The most frequently used field data to infer recognition in males have been measures of reduced aggression in response to playback of recorded neighbour song compared with the songs of strangers (Stoddard 1996).

Besides territorial defence, male song is also thought to function in the attraction and stimulation of a mate (Searcy & Andersson 1986; Catchpole 1987; Kroodsma & Byers 1991). Female reactions to song are usually investigated using methods based on the copulation solicitation displays adopted by oestradiol-treated females in response to recorded male song (Searcy 1992a). However, to date only one study has used this technique to demonstrate that female songbirds discriminate among categories of local males. Female song sparrows, *Melospiza melodia*, have been shown to solicit more frequently and more intensely to playback of songs recorded from the repertoires of their mates than to songs recorded from local strangers (O'Loghlen & Beecher 1997).

An alternative to mate recognition as an explanation for female preferences for mate songs shown in the previous study is familiarity. Mate songs may be preferred simply because females have had more exposure to these songs than to songs of strangers. In the present study we tested this hypothesis by comparing female responses to songs of mates, neighbouring males and strangers.

Male and female song sparrows aggressively defend their territory against intrusion from neighbouring males using both visual and acoustic signals (Nice 1943; Elekonich 1997). As with most oscines, in general only male song sparrows sing in these circumstances. Males also sing spontaneously prior to and during the breeding season when they are not obviously involved in interactions with neighbouring males (Nice 1943). Thus, female song sparrows are likely to have extensive social contact and exposure to the songs of their mates and those of neighbouring males. If female preferences for mate songs shown in the previous study are based solely on exposure levels, then females would show equivalent levels of responsiveness to songs of neighbours and mates.

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Female solicitation displays adopted in response to playback of neighbour song are also of interest in another context besides individual recognition. Extrapair fertilizations have been detected in the majority of oscines investigated to date (Birkhead & Møller 1992), including song sparrows at our Washington study site (C. E. Hill, unpublished data) and another local population (Keller 1996). In many species, males in neighbouring territories are most likely to be responsible for extrapair fertilizations (Gibbs et al. 1990; Westneat 1992, 1993; Stutchbury et al. 1994; Wetton et al. 1995; Whittingham & Lifjeld 1995; Yezerinac et al. 1995; Gray 1996; Hasselquist et al. 1996; Perreault et al. 1997). Whether this is the case with song sparrows has not been determined yet. Song has been implicated in female choice of extrapair partners in a number of species (Eens et al. 1991; Hasselquist et al. 1996) and in song sparrows, females have been shown to discriminate in their sexual displays in response to playback of conspecific song (Searcy 1984; O'Loghlen & Beecher 1997). Thus evidence from the current study on whether neighbouring males have songs that are especially sexually stimulating to females are likely to be pertinent to studies of mate choice in song sparrows.

In our study population, male song sparrows typically have repertoires of 5–13 different song types. The set of song types in a male's repertoire is generally unique, but some of his songs or similar types may be present in repertoires of one or more other males in the population, particularly males in neighbouring territories (Beecher et al. 1994a; Nordby et al. 1999); we refer to these similar songs as matching songs. We excluded matching songs from our set of neighbour playback songs because female responses to these songs could be based either on recognition of songs of neighbours per se, or because these songs sound like the songs of their mates.

Matching or sharing of song types among local males may be important in a context other than extrapair copulations. It has been suggested that female preferences may explain, at least in part, why local males share song types. The deceptive mimicry hypothesis (Payne 1981) proposes that young males may benefit in their interactions with local females by copying the songs of older, established males in an area. Young males that sound like local adult males may be more successful in attracting local females.

We wanted to investigate this possibility that females are more stimulated by songs that are similar to their mates', or that match types in their mates' repertoires, than by nonmatching songs. Again, as in the neighbour song playback experiment there was the possibility of a confounding effect if we used matching songs recorded from neighbours. Thus we compared female responses to matching songs recorded from stranger males with responses to mate and nonmatching stranger song types.

METHODS

Twenty-one female song sparrows were lured into mist nets or seed-baited Potter traps, using a caged male song sparrow as a decoy and playback of male and/or female song sparrow vocalizations in Discovery Park, Seattle, Washington, from 13 February to 3 April 1996 (12 females), or 23 February to 1 April 1997 (nine females). All females were trapped on territories of previously banded males and were observed co-defending or feeding alongside the resident males prior to capture. Four pairs of females had the same mate. In three of these cases, a different female replaced a mate between 1996 and 1997; in the remaining case, a new female replaced the first female after the latter had been removed for testing in the laboratory. We transported females to the University of Washington immediately after capture. On the day of capture, we inserted a Silastic tube (1.69 outer diameter, Dow Corning, Midland, Michigan) packed with a 10-mm length of oestradiol under the skin on the chest of each bird.

Housing and feeding were as described in O'Loghlen & Beecher (1997). Females were released at their site of capture when tests were completed.

Playback Recordings

We prepared audiospectrograms on a Kay DSP-5500 sonagraph for songs recorded prior to 1997 and on a Vektron Pentium 75-MHz computer using Syrinx© software for the 1997 recordings. We used these spectrograms to classify the songs of each male as different types (Stoddard et al. 1988; Searcy et al. 1995). Songs used as playback stimuli to test the females were chosen for recording quality and equivalent duration. Recordings of these songs were passed through a high-pass filter set at 1500 Hz and digitally sampled at 22 kHz/s. Peak amplitudes were standardized and the songs stored as wave files on a Vektron Pentium 75-MHz computer.

All males were recorded using either a Sony Professional Walkman cassette recorder and Sennheiser MKH 816T directional microphone, or a Sony TC-D5M recorder and Sennheiser M88 microphone. We recorded all mates and neighbouring males in the field on two or more occasions. Each bird was recorded for a minimum of 2 h using playback of song sparrow songs to stimulate singing. This level of recording effort is usually sufficient to reveal a male's complete song repertoire (C. R. Wilkinson, M. D. Beecher & J. C. Nordby, unpublished data).

We categorized songs used as stimuli as Mate, Nonmatching Neighbour (NN), Matching Stranger (MS), or Nonmatching Stranger (NS). Songs recorded from 17 different males on whose territories females were trapped, were included in the Mate category. Songs of 14 banded males resident in territories adjacent to territories where females were trapped were used as Neighbour stimuli. Neighbouring males were observed on their territories at the time females were captured. Songs recorded from six of these males were used as Neighbour playback for two females each, and no Neighbour songs were available for one female. Eleven of these Neighbour males were also mates of females participating in the experiment. Ten females were trapped from pairs of adjacent territories and songs of their mates served both as Mate and Neighbour stimuli in a reciprocal manner.

We used two categories of stranger songs, Matching Stranger and Nonmatching Stranger. Nonmatching songs were recorded from living males whose territories were far removed (>500 m) from the territory of a female's mate. Only song types that did not match any of the known types in the repertoire of a female's mate were included. Fourteen songs recorded from 14 different males were used as NS playback.

Matching Stranger songs were chosen from a library of songs recorded from 25 different Park males between 1986 and 1997 and included songs of both living and dead males. MS songs recorded from a living or recently deceased male were used only if the male had resided in a territory far removed (>500 m) from that of a female's mate. Based on audiospectrograms, one of us (A.O'L.) chose MS songs that were structurally similar to song types in the repertoires of mates. After all females had been tested, MS songs and their putative matching mate songs were independently evaluated by three judges (excluding A.O'L.) with experience in evaluating songs for matching and scored for closeness of match on a scale of 0–10. Scores were based on visual assessment of structural similarities of notes and on note syntax. Zero score was awarded to a song with no structural similarities to its putative matching mate type, and 10 to a near perfect match.

Playback Procedures

Females were first tested for their reactions to songs 10–14 days after they received their implants. Their responses were recorded on VHS video cassettes. In general, subjects were presented with four different songs from each of the four stimulus categories, for a total of 16 different songs. Eight different songs, two from each category, were presented per day on two consecutive days. If a female did not respond to any stimulus on one or both of these days, trials for those days were repeated on the following 1–2 days. If a female did not respond on all 4 days, she was considered a 'nonresponder'. There were some exceptions to the above procedures. MS songs were available for only 14 females and three of these heard only three MS songs. No Neighbour songs were available for one female. Another female gave no response during her first 2 days of testing and she was retested after a gap of 2 days.

All playback trials consisted of eight repetitions of a single song type with each repetition separated by 10 s of silence. This is similar to the way in which song sparrows sing in the wild except that we did not use the within-song type variations heard in the wild. In nature, song sparrows sing each song type a number of times before switching to another type. However, song sparrows also generally introduce some structural variation into each repetition of a type (see Stoddard et al. 1988; Searcy et al. 1995). Playbacks were separated by approximately 1 h and the order in which the first four categories were played on the first test day was determined by a draw. This order was repeated for the second four trials on the first day and reversed for trials on the second day. Song playbacks were played from wave files on the Pentium computer using a Windows Command Line batch file and a Sound Blaster 16 (Creative Labs, Inc., Milpitas, California) sound card with the volume set at a standard amplitude.

Data Analysis

We determined the number and duration of copulation solicitation displays from the videotapes played at slow speed. Extension and retraction of the wings were used to indicate the start or finish of a display. This method of assessing female responses gives clear and unambiguous results; in a previous study using this method, there was 100% agreement between an independent judge and the authors on the number of female responses to each test stimulus (O'Loghlen & Beecher 1997).

We analysed two response measures. First, we calculated the proportion of songs in each category that elicited at least one display in a playback (eight repetitions of a song) for each female (e.g. a female scored 1.0 if she responded at least once to each of the four neighbour songs presented). Second, we divided the total duration of solicitation postures for each song category by the number of song types presented in that category to give average total duration per playback (eight repetitions of a song). Playbacks that did not elicit a response were scored as zero duration.

A previous study had shown that for both of these response measures, Mate songs were significantly more stimulating for females than Nonmatching Stranger songs (O'Loghlen & Beecher 1997). In the current study we were interested specifically in comparing how females responded to these two categories with how they responded to two additional categories, Nonmatching Neighbour and Matching Stranger songs. We predicted that females would respond to Nonmatching Neighbour and Matching Stranger songs at a level intermediate to their response to Mate song (strongest), and Nonmatching Stranger song (weakest). We had no basis for predictions concerning differences between Nonmatching Neighbour and Matching Stranger songs. Thus comparisons between the latter two categories were not included in our planned pairwise analyses.

We used Kolmogorov–Smirnov tests to compare the two annual samples. We used Friedman ANOVA chi-square tests to detect significant response differences among song categories in each of the two sets of multiple comparisons (Mate, NN, NS, and Mate, MS, NS) and Wilcoxon signed-ranks tests for pairwise comparisons.

Scores for structural similarity between mate songs and stranger songs chosen as matches were significantly correlated among the three judges (Kendall coefficient of concordance: $W=0.10$, $N=53$, $P<0.001$) and judges' scores were averaged for each matching song. Average matching scores were compared with female solicitation responses using a Spearman rank correlation. All probabilities are two-tailed. Statistica software was used for all statistical analyses.

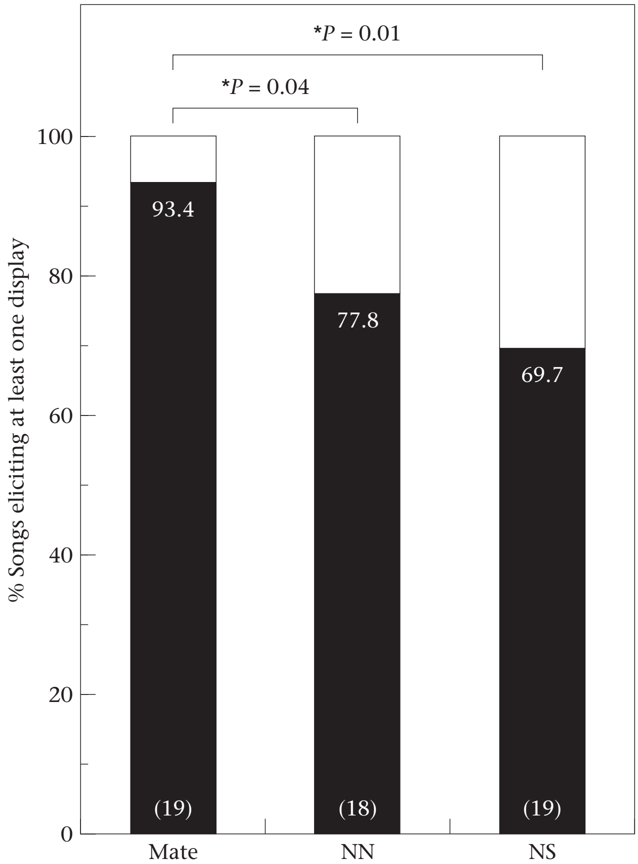

Figure 1. Percentage of songs in Mate, Nonmatching Neighbour (NN) and Stranger (NS) categories that elicited at least one solicitation display during playbacks. Playbacks consisted of eight repetitions of a song, each separated by 10 s of silence. Numbers of females are shown in parentheses. In general each female was presented with four songs from each category (see text for exceptions). *Wilcoxon signed-ranks test.

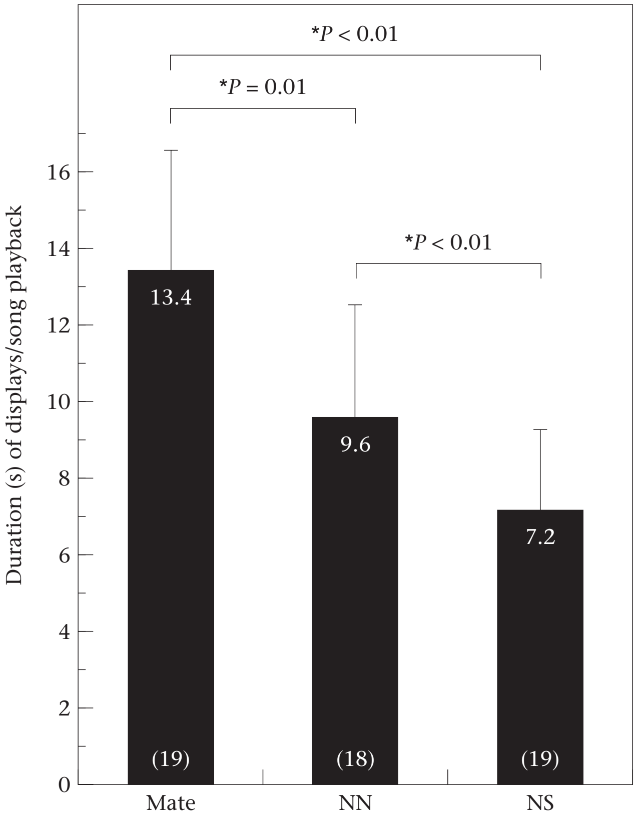

Figure 2. Mean (+SE) total duration of solicitation displays during playback of eight repetitions of a song in Mate, Nonmatching Neighbour (NN) and Stranger (NS) song categories. Other details as in Fig. 1. *Wilcoxon signed-ranks test.

RESULTS

One female each from the 12 trapped in 1996 and the nine trapped in 1997 did not respond to any of the test stimuli; these two females were excluded from analyses (one was the replacement mate trapped on a male's territory during 1997, see above). There were no significant differences between years in the solicitation display measures in each of the test song categories (Kolmogorov–Smirnov tests: all NS) and data from both years have been combined for analyses.

Mate, Nonmatching Neighbour and Nonmatching Stranger Songs

Mate, Nonmatching Neighbour and Nonmatching Stranger song categories differed significantly in the probability that females would give at least one copulation solicitation response during playback (Friedman ANOVA: χ^2_2=8.05, N=18, P<0.02; Fig. 1). Females gave at least one solicitation response during the playback trial most often when a Mate song was presented (71/76 songs, 93.4%). Females were less likely to respond if the song was an NN song (56/72, 77.8%), or NS song (53/76, 69.7%). In pairwise comparisons, Mate song was significantly more likely to elicit a response from females than nonmatching song from either neighbouring males (Wilcoxon: T=2, N=18, P=0.04), or strangers (Wilcoxon: T=2.5, N=19, P=0.01). Nonmatching song types recorded from neighbours and strangers did not differ significantly in this response measure (Wilcoxon: T=17.0, N=18, P=0.28).

Solicitation displays elicited with song playback ranged from a brief crouch and wing flip lasting 0.2 s to a full posture lasting almost 10 s, with the average display lasting 3.7 s (Fig. 2). Females differed significantly in their responses to the three categories of songs (Friedman ANOVA: χ^2_2=19.8, N=18, P<0.001). In pairwise comparisons, females displayed significantly longer during Mate playbacks (median 6.6 s, range 1.2–47.6 s) than during NN playbacks (median 5.1 s, range 0–41.0 s; Wilcoxon: T=29.0, N=18, P=0.01), or NS playbacks (median 3.4 s, range 0–31.1 s; Wilcoxon: T=1.0, N=19, P<0.01). Furthermore, nonmatching songs recorded from neighbours were significantly more stimulating to females than NS songs (Wilcoxon: T=12.0, N=18, P=0.01).

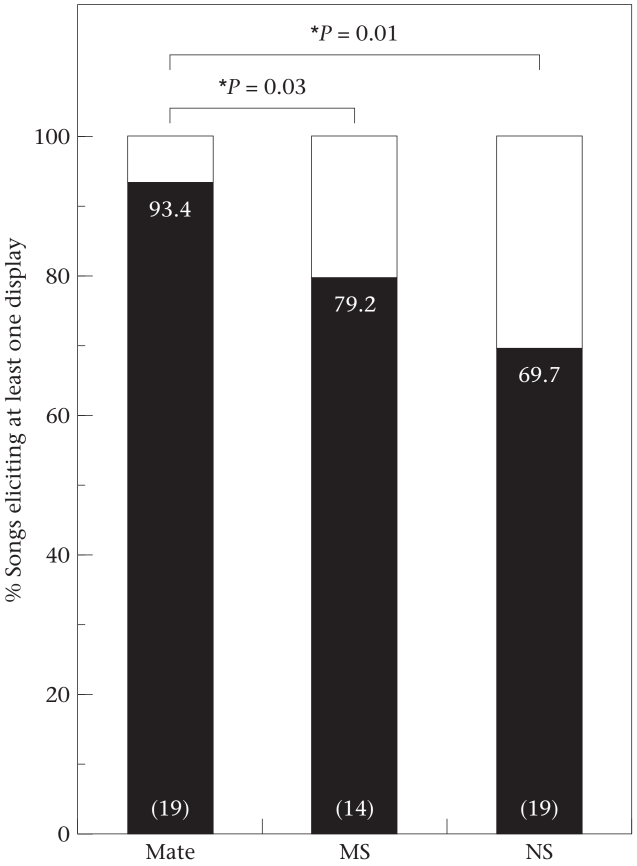

Figure 3. Percentage of songs in Mate, Matching Stranger (MS) and Nonmatching Stranger (NS) categories that elicited at least one solicitation display during playbacks. Playbacks consisted of eight repetitions of a song, each separated by 10 s of silence. Numbers of females are shown in parentheses. In general each female was presented with four songs from each category (see text for exceptions). *Wilcoxon signed-ranks test.

Mates, Matching Stranger and Nonmatching Stranger Songs

The probability that a female would perform a solicitation display at least once during a playback differed significantly between Mate, MS and NS categories of songs (Friedman ANOVA: χ^2_2=6.20, N=14, P<0.05). The proportion of MS songs eliciting at least one response (42/53, 79.2%), was intermediate between equivalent results for Mate and NS songs (93.4 and 69.7%, respectively; Fig. 3). Pairwise comparisons showed that MS song was less likely than Mate song to provoke at least one response during playback (Wilcoxon: T=0.0, N=14, P=0.03). There was no significant difference in the likelihood that a Matching or Nonmatching Stranger song would produce at least one response (Wilcoxon: T=13.0, N=14, P=0.48).

Average total duration of displays during playback differed significantly by type category (Friedman ANOVA: χ^2_2=14.3, N=14, P<0.001). Differences in average total response duration between Mate (median 6.6 s, range 1.2–47.6 s) and MS (median 4.4 s, range 0.7–30.9 s) were significant at the 0.05 level for a one-tailed but not a two-tailed test (Wilcoxon: T=27.0, N=14, P=0.10), undoubtedly related to the smaller sample size for this comparison (Fig. 4). Finally, MS songs were significantly more stimulating to females than NS songs (Wilcoxon: T=6.0, N=14, P=0.01).

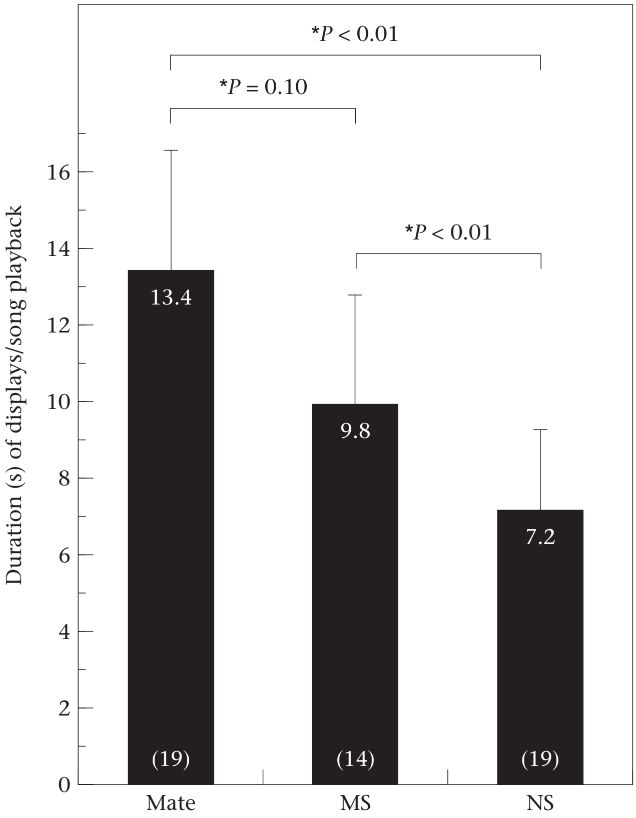

Figure 4. Mean (+SE) total duration of solicitation displays per playback in Mate, Matching Stranger (MS) and Nonmatching Stranger (NS) song categories. Other details as in Fig. 3. *Wilcoxon signed-ranks test.

Similarities between Mate and Matching Stranger Songs

The mean score awarded by the three judges for structural similarity between matching Mate and Stranger songs was 7.2, with a median score of 8 (range 2.7–10), out of a maximum of 10 for a near perfect match. Average matching score for each MS playback song was significantly correlated with the number of displays the song elicited when it was played to a female (Spearman rank correlation: r_s=0.30, N=53, P<0.03). Thus, females were more likely to respond to songs that more closely matched a song in their mate's repertoire than to songs that were less similar.

DISCUSSION

Songs of Mates, Neighbours and Strangers

Our study demonstrates that female song sparrows have the ability to discriminate between males on the basis of the males' songs. This ability is similar to that shown by male song sparrows (Stoddard et al. 1991) and by males in other oscine species (review in Stoddard 1996). As observed in a previous study (O'Loghlen & Beecher 1997), female song sparrows show sexual preferences for song types recorded from the repertoires of their mates over songs recorded from strangers. The present study demonstrates additionally that females prefer mate songs over nonmatching songs of males living in neighbouring territories, and in turn, prefer these neighbour songs over those of strangers resident in more distant sites in the local population. Thus, female song sparrows show discrimination based on song between three categories of males: mates, neighbours and strangers.

We interpret the current results as evidence that female song sparrows can recognize individual males by the song types in their repertoires. Thus it is parsimonious to conclude that female song sparrows have recognition abilities similar to those already demonstrated in male song sparrows (Stoddard et al. 1991). It could be argued that discrimination revealed in our study was the result of variation in levels of females' exposure to the different categories of songs. Clearly females will have had more exposure to the songs of mates and neighbours than to the songs of strangers. However, exposure to mate and neighbour songs should be similar.

Frequent and intense social interactions between neighbouring male song sparrows provide female mates with high levels of exposure to both their mates' songs and their neighbours' songs. Song sparrow territories in Discovery Park have been estimated at 50 m in diameter on average (C. E. Hill, unpublished data). Male song sparrows sing loudly and persistently to attract mates, and when establishing and defending territories. Cassidy (1993) calculated a rate of 100 songs/h based on a sample of 44 males recorded singing spontaneously over a period of 2–3.5 h in the wild. The majority of these males (75.0%) sang their entire repertoire of song types during this period. Furthermore, both female and male song sparrows frequently interact aggressively with neighbouring males at territorial boundaries and such disputes usually involve prolonged bouts of singing and countersinging by both mate and neighbouring males. Song rates of over 200/h have been reported under these circumstances (Nice 1943; Mulligan 1966). Thus, female exposure to the songs of mates and neighbouring males may differ to some extent, but in both cases exposure is likely to be extensive. Song memorization in captive male song sparrows can occur after exposure to a single bout of 30 repetitions of a recorded song (Peters et al. 1992). Even if the minimum threshold of exposure necessary for song memorization by females is greater than that for males, this threshold is most likely exceeded by the individual singing of the mate and the neighbouring males.

Matching Stranger Songs

Females were more responsive to stranger songs that were similar to song types in their mates' repertoires than to song types that were not similar. Furthermore, the greater the similarity between the stranger's and mate's song, the more likely the female was to respond to it.

The most parsimonious explanation for female reactions to these mate-like songs is that females were simply confused about the identity of the singer, that is, they responded as if it were their mate singing. There is evidence that similarity between songs can also confuse male song sparrows. Stoddard et al. (1991) have shown that male song sparrows can discriminate established neighbours using both shared and unshared songs. However, in operant song classification studies in the laboratory, males initially confused similar song types (Beecher et al. 1994b). Males eventually learned to discriminate between similar songs but it took them considerably longer to learn to discriminate between these songs than between dissimilar songs.

Deceptive mimicry has been proposed as a model to explain the persistence of song sharing among territorial males (Payne 1981). Under this model, a male is thought to benefit from learning to mimic the songs of local resident males when trying to establish a new territory. One proposed advantage of acoustic mimicry to the new male results from the confusion and reduced aggression provoked from residents by singing locally shared song types (McGregor & Avery 1986; Beecher et al. 1994b).

This model also proposes that locally shared songs are beneficial to males in attracting mates (Payne 1981). Females may be preferentially attracted to males with locally shared songs. Individuals that sing these songs are likely to have established territories and on average to be older, more experienced males (Yasukawa et al. 1980; Loffredo & Borgia 1986; Rothstein & Fleischer 1987; Eens et al. 1991; O'Loghlen & Rothstein 1995). Furthermore, under these circumstances, natural selection is expected to favour young males that learn local neighbourhood songs when setting up a territory. These young males should have an advantage in attracting females because they sound like older males in the area.

In song sparrows, males with song types that are similar to those sung by mated males in a local neighbourhood are likely to have an advantage in sexual interactions with local females compared with males that lack such songs. This is true whether the males are strangers or neighbours and is consistent with the female mate choice component of the deceptive mimicry model (Payne 1981). Other features of our study population are also consistent with this model. For example, song sharing occurs in small groups of socially interacting territory holders rather than the larger groups of individuals that characterize dialects in other species (Beecher et al. 1997). Song types involved in sharing are not constant over time and in any year-to-year comparison, different types may be shared within the local group (Payne 1996). Recent studies of song ontogeny in males from our study population are also consistent with the 'open' vocal ontogeny prediction of the deceptive mimicry model (J. C. Nordby, S. E. Campbell, J. M. Burt & M. D. Beecher, unpublished data).

Sharing songs with a neighbour may be of benefit to a male in another context. It has been suggested that song preferences shown by females in solicitation studies may reflect the circumstances under which females choose extrapair partners in nature (Møller 1991; Searcy 1992b). Support for this notion comes from studies of great reed warblers, *Acrocephalus arundinaceus*. Female great reed warblers solicit more in response to large-syllable repertoires (Catchpole et al. 1986), and in the wild, choose males with large-syllable repertoires as extrapair partners (Hasselquist et al. 1996).

Song sparrows are apparently monogamous. However, a recent study, using DNA analysis of paternity in a sedentary island population in British Columbia, found that 23.4% of broods (21 of 91 broods) contained extrapair offspring, and 15% of all offspring examined were not the progeny of the social mate (Keller 1996). Initial results from an on-going paternity study in our population also show evidence of extrapair fertilizations (C. E. Hill, unpublished data). Although extrapair fathers have not yet been identified in either of these studies, the most frequently observed pattern in passerines is that neighbouring males are most likely to be extrapair fathers (Gibbs et al. 1990; Westneat 1992, 1993; Stutchbury et al. 1994; Wetton et al. 1995; Whittingham & Lifjeld 1995; Yezerinac et al. 1995; Gray 1996; Hasselquist et al. 1996; Perreault et al. 1997). Sexual responses of female song sparrows to the nonmate-matching songs of neighbouring males in the present study suggest that neighbouring males would have distinct advantages over other males in obtaining extrapair copulations. Furthermore, it would seem reasonable to expect preferential responses by females to the matching song types of neighbours. An interesting question for future investigation is whether the combination of these two categories of stimuli found in the matching songs of neighbours has a synergistic effect on female responsiveness.

Conclusions

Our results suggest that female song sparrows can recognize individual male conspecifics by the song types in their repertoires. The study also identifies two new categories of female sexual preferences for male song: songs of males resident in neighbouring territories and songs that are structurally similar to types in the repertoires of mates. Whether these preferences affect mate choice in nature has not yet been determined. On-going investigations of extrapair paternity in our study population may help to shed some light on the function of these preferences. Finally, we suggest that further insights into the significance of female song preferences may come from studies of the ontogeny of these preferences.

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