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Sexual preferences for mate song types in female song sparrows

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Abstract. Copulation solicitation displays were used to investigate whether female song sparrows are especially stimulated by the songs their mates sing. Eight of nine (88.9%) recently captured oestradiol-treated female song sparrows, *Melospiza melodia*, gave more solicitation displays and displayed more intensely for song types recorded from repertoires of their mates than for songs from other males from the local population. This is the first study to show female sexual preferences for mate song in songbirds and to demonstrate that female song sparrows discriminate in their sexual responses based on song types. It is not known whether these song preferences influenced females' choice of mate in the field or arose after pair formation. Regardless of origin, especially stimulating songs are likely to be important to the reproductive behaviour of females and could influence the mating success of males.

It is generally accepted that one of the functions of song in male songbirds is attraction and stimulation of a mate (Searcy & Andersson 1986; Catchpole 1987; Kroodsma & Byers 1991). Evidence to support this assumption includes results from a number of laboratory studies that used the copulation solicitation displays adopted by females of some species in response to recorded song (Searcy 1992a). In most species studied to date using this procedure, females have shown sexual preferences for certain categories of song and in general, have been more responsive to species- and population- typical conspecific songs (King & West 1977; Baker et al. 1981; Searcy & Marler 1981; O'Loghlen & Rothstein 1995). The discrimination shown by females under these laboratory conditions is likely to be important in nature because these preferences are expressed in a direct mating context (Searcy 1992a). Thus males whose singing behaviour is especially sexually stimulating for females are likely to enjoy some reproductive advantage. Studies of *Acrocephalus* warblers and of brown-headed cowbirds, *Molothrus ater*, have provided experimental evidence to support this conclusion (Catchpole 1987; West et al. 1981).

In two key circumstances, sexual biases for certain learned songs could theoretically affect female mate choice (Searcy 1992b). Pre-existing preferences for particular songs could influence a female's choice of mate, and song preferences that develop as a result of association with a particular male may be important in the establishment and maintenance of pair bonds. These possibilities are not mutually exclusive. For example, song preferences that develop as a result of association with one male could influence future mate choice. Thus, irrespective of origin, female sexual preferences for certain songs are likely to have consequences for male reproductive success.

In the present study we investigated whether female song sparrows, *Melospiza melodia*, have sexual preferences based on song types. Male song sparrows generally have repertoires of five to 13 different species-typical song types that they learn from conspecifics in the population where they establish their breeding territories (Cassidy 1993; Beecher et al. 1994a). Males use their songs to interact with other males in territory acquisition and defence (Kramer et al. 1985). In addition, recorded conspecific song can stimulate oestradiol-treated female song sparrows to perform sexual displays, suggesting a role for song in mate attraction and stimulation (Searcy & Marler 1981). Furthermore, females show preferences for playback of multiple song types versus repetitions

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of a single type, suggesting that repertoire size may also influence female reproductive behaviour (Searcy 1984). However, there have been no studies of female sexual responses to song types that characterize the repertoire of individual male song sparrows.

We used copulation solicitation displays elicited from recently captured female song sparrows that had been treated with oestradiol to investigate whether females prefer song types from the repertoire of their mate over song types of other males from the same population. In our study population, the complement of song types in a male's repertoire is generally unique, although some of these types may be present in repertoires of one or more other males in the population, particularly males with neighbouring territories (Beecher et al. 1994a). In general, the non-mate song types we used to test females did not match types in the repertoires of the females' mates. Females received no song exposure while in captivity, to ensure that any preferences shown would be a result of their social and learning experiences in nature.

METHODS

Nine female song sparrows were trapped in seed-baited Potter traps (three females) or lured into a mist-net (six females) with playback of male song or female vocalizations in Discovery Park, Seattle, WA from 4 February to 4 April 1995. All females were trapped in territories of banded males and three females had been previously banded in autumn 1994. Females were observed either feeding alongside or co-defending with the resident male immediately prior to capture. Behavioural observations and wing chord length (<64 mm for females) were used to determine sex. Females were taken to the University of Washington immediately after capture, where they received unique combinations of three plastic leg bands and one metal Fish and Wildlife band. Silastic tubes (Dow Corning, 1.69 mm outer diameter) packed with a 10 mm length of oestradiol (Sigma) were inserted under the skin on the chest of each bird on the day of capture.

Female W4 received two implants, the second 13 days after the first. Birds were housed in separate cages (28 × 23 × 22 cm), which were placed inside individual sound attenuation chambers (external dimensions=48 × 50 × 50 cm). Each chamber was fitted with a light, 10-cm Realistic speaker and a viewing window (diameter=50 cm) designed to take a wide-angle video lens. Birds were maintained in the chambers on a 16:8 h light:dark photoperiod throughout the experiment. Handling and feeding (Mazuri kibble and seed mixture ad libitum plus mealworms) was identical for all birds. Females W1 and W3 did not become responsive to song playback; after 23 and 24 days, respectively, their implants were removed, and they were placed in separate outdoor aviaries (2 × 1.5 × 2 m). Approximately 6 weeks later, these two females received new implants, and were tested 10 days subsequently as described below. Females were released at their site of capture when tests were completed.

Playback Recordings

Songs used as mate playbacks were recorded during 1994 breeding and late summer seasons using a Sony Professional Walkman cassette recorder and Sennheiser MKH 816T directional microphone. Each male was recorded on a number of occasions. Audiospectrograms were prepared from these recordings on a Kay DSP-5500 Sonagraph and used to categorize songs by types (Stoddard et al. 1988; Searcy et al. 1995). We used 26 songs recorded from 20 males as non-mate playback. None of these males were or had been resident in territories neighbouring those in which test females were captured. Non-mate songs were obtained from a library of digitized songs recorded from banded males in Discovery Park between 1986 and 1994. The majority of these non-mate songs, or variants of them, are known to have be included in repertoires of males resident in the Park at the time of the study (M. D. Beecher, unpublished data).

Songs used for playback were chosen for recording quality and equivalent duration. Songs were passed through a high-pass filter set at 1500 Hz and digitally sampled at 22 kHz. Peak amplitudes were standardized and songs stored as wave files on a Gateway 386-16 SX computer.

Playback Procedures

We tested females for responses to songs 12–15 days after they received their implants and recorded their reactions on VHS videocassettes.

Seven subjects were presented with 12 different song types over 2 days, six from the repertoires of their mates and six from the pool of non-mate songs. We played three different mate and non-mate song types to each of these seven on each test day. Because of technical difficulties, the remaining two subjects (W2 and W4) were presented with playbacks over 3 consecutive days. W2 heard four playbacks on day 1, six on day 2 and four on day 3; W4 heard 10 playbacks (five mate and five non-mate): four, four and two types on consecutive days.

A playback consisted of eight repetitions of a song type with each repetition separated by 10 s of silence. This sequence 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 nature. In nature, song sparrows utter each song type a number of times before switching to another type, varying each repetition of a type slightly (Stoddard et al. 1988; Searcy et al. 1995). Playbacks were separated by approximately 1 h, and the category (mate versus non-mate) of the first playback of the first test day was determined by tossing a coin. The first playback on the second day was from the opposite category of that used as first on day 1. Song categories were alternated during a test day. Song playbacks were played from wave files on a 386 computer using an MS DOS batch file and a Sound Blaster 16 sound card (Creative Labs, Inc.) with the volume set at a standard amplitude.

Data Analyses

We determined number and duration of copulation solicitation postures from the videotapes played at slow speed. Average number of postures for mate and non-mate songs was calculated for each bird by dividing total number of postures adopted by number of different song types presented from each of these categories. Average duration of postures was calculated by dividing the total time each female spent in solicitation postures in response to mate and non-mate playbacks by the number of different song types in each category. Playbacks to which there was no response were included as zero duration. Wilcoxon matched-pairs signed-ranks tests were used to compare average number and duration of responses to mate and non-mate song types, and a sign test used to compare number of individuals responding more often to mate than to non-mate songs. All probabilities are two-tailed.

The intensity of female response was measured by scoring postures adopted by females. A full solicitation posture with wings extended and vibrating, head arched back and tail elevated above 180° was awarded a score of 3; postures consisting of extended wings and elevated tail scored 2; a score of 1 was given for extended, vibrating wings. Generally extension and retraction of the wings was used to indicate the start or finish of a posture. Playbacks to which there was no response received a score of 0. O'Loghlen & Rothstein (1995) found a correlation between display duration and posture score in a study of female brown-headed cowbirds. Duration is a more objective and accurate measure of responses, and we looked for an equivalent correlation in female song sparrows using a Spearman rank-order correlation coefficient for mean score and duration per female based on all playbacks.

RESULTS

All nine females adopted pre-copulatory postures on at least one occasion during playback of songs recorded from their putative mates, and seven females did so for at least one non-mate song as well. Overall, each female gave a mean of 21.9 solicitation displays (median=17, range=2–64) during the trials. Females displayed at least once during 60 of the 106 total playback trials (56.6%), and, on average, to 4.0 of the mate song types and 2.7 of non-mate types presented (Wilcoxon matched-pairs signed-ranks test: $T^{+}=15.0$, $N=9$, $P=0.06$, medians=5 and 3 types, respectively, ranges=1–6 and 0–6, respectively).

Besides this tendency to be more likely to respond to mate song, females performed almost twice as many solicitation displays during mate song types (14.1 mean postures per female) than during non-mate types (7.8 postures; Wilcoxon matched-pairs signed-ranks test: $T^{+}=42.0$, $N=9$, $P=0.02$, medians=12 and 3 postures respectively; ranges=1–47 and 0–23, respectively). Eight of the nine females gave more solicitation displays for mate songs (sign test: $N=9$, $P=0.04$; Fig. 1). Female W3, the only female to show a preference for non-mate song, gave three responses, two to one non-mate song type and one to a mate song. W3 was one of the two females that did not

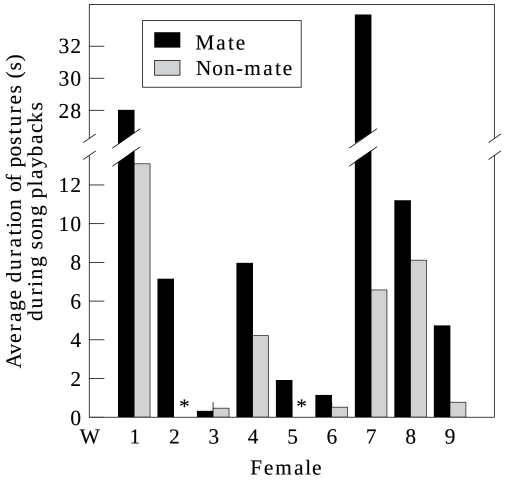

Figure 1. Average number of solicitation postures adopted by each female in response to playback of mate and non-mate songs. Females were presented with six song types from the repertoires of their mates and six non-mate song types each from the repertoire of a different male (five of each type for W4). During a playback, a song type was repeated eight times with 10-s gaps. Averages were calculated by dividing total number of postures for mate and non-mate songs by 6 respectively (5 for W4), the number of different song types in each of these categories. Average number of postures was significantly greater ($P=0.01$) for mate than non-mate song types (Wilcoxon matched-pairs signed-ranks test). *Indicates no responses.

become responsive when first taken into captivity and was held in captivity for several weeks prior to being tested again (W8 was the other).

Twenty-six song types recorded from 20 males were presented to females as non-mate songs, and 17 (65.4%) of these types elicited a response on at least one occasion.

An independent observer, unaware of the playback categories, viewed the videotapes of four females chosen at random from our sample of nine birds. There was 100% agreement by this observer with the number of displays we reported for these birds.

There was a highly significant correlation between mean duration and mean score per female for solicitation postures elicited in response to mate and non-mate songs (Pearson rank-order correlation coefficient, $r_s=0.97$, $N=18$, $P<0.001$); therefore we have used duration as a measure of response intensity. Each playback consisted of eight repetitions of a song type, and on average females maintained postures for almost three times as long during presentations of mate song (mean=10.6 s) than during non-mate song (3.7 s; Wilcoxon matched-pairs signed-ranks test: $T^+=43.0$, $N=9$, $P=0.01$, medians=7.0 and 0.8 respectively; ranges=0.2–33.7 and 0–13.1, respectively; Fig. 2).

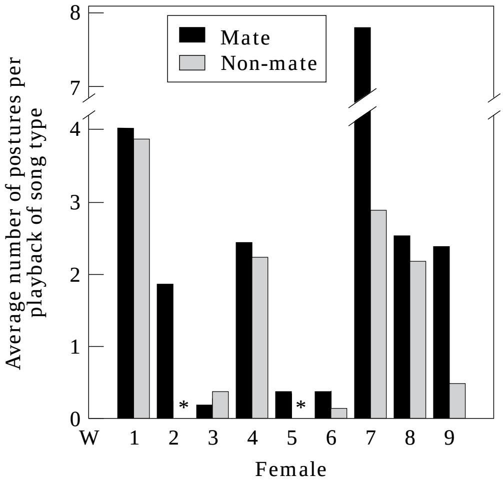

Figure 2. Average duration of solicitation postures adopted in response to playback of mate and non-mate song types by each female. Females were presented with mate and non-mate songs as described in Fig. 1. Average duration was calculated by dividing total time females held display postures during playback of mate and non-mate song types by 6 (5 for W4) respectively. Average duration of displays during mate song was significantly greater ($P=0.01$) than during non-mate songs (Wilcoxon matched-pairs signed-ranks test). *Indicates no responses.

DISCUSSION

Results from this study demonstrate that female song sparrows are more readily stimulated to perform sexual displays when presented with song types from the repertoires of their mates than songs from other males in the local population. Furthermore, female responses to mate song types are more intense than responses elicited by non-mate song types. Female song sparrows appear to recognize song types in the repertoires of their mates and show preferences for these types in a direct reproductive context.

Recognition of mate song has been shown in two other species. During their fertile period, female dunnocks, *Prunella modularis*, will preferentially approach playback of mate song versus that of neighbours, apparently seeking copulations (Wiley et al. 1991). Captive zebra finches, *Taeniopygia guttata*, also show mate recognition by approaching playback of their mate's song (Miller 1979). However, we know of no studies of songbirds where females have shown explicit sexual preferences for mate songs. The sexual nature of female responses shown in the current study suggests that these preferences could have important repercussions for reproductive success. Male song can stimulate female reproductive physiology (Hinde et al. 1974; Hinde & Steel 1976, 1978; Kroodsma 1976; Morton et al. 1985) and mating behaviour (Kroodsma 1976; Logan 1983) and may function to synchronize reproductive behaviour between mates (Logan 1983). Selection should favour mechanisms that ensure that this stimulation results from the singing behaviour of a female's mate rather than as an incidental effect of the singing of other males (e.g. neighbours). Especially stimulating songs are likely to be important in maintaining pair bonds, ensuring mate fidelity and increasing the fertilization success of copulations.

This is the first study to show that female song sparrows have sexual preferences for specific types of conspecific songs. Searcy (1984) demonstrated that female song sparrows will solicit more intensely to playback of multiple song types than to repetition of a single type. This effect is evidently a result of switching song types within a playback sequence, however, and is not dependent on song type per se. We cannot distinguish from our results whether females preferentially responded to mate song types because females recognized these types as belonging to their mates, or simply because of familiarity with these types. In the latter case, females should preferentially respond to any song types to which they have had sufficient exposure, regardless of the identity of the males that produced the songs. In other species where females have shown selectivity in their responses to song, familiarity does not appear to have been the basis for discrimination (Miller 1979; West & King 1980; Wiley et al. 1991). We will address this question of familiarity more directly in future studies of song preferences in female song sparrows.

Female discrimination between mate and nonmate song types could have been based on recognition of some 'voice' characteristic or 'signature' trait that distinguishes the songs of each individual male (Beecher 1989) and enables recognition of a male regardless of the song types he sings. Some experimental evidence argues against this explanation. In a laboratory study of song perception in song sparrows, Beecher et al. (1994b) demonstrated that song sparrows did not use individual voice characteristics to distinguish songs of different males. That study included one female, and her ability to recognize and categorize song types equalled that of males in the study: none of the subjects were able to categorize songs on the basis of a distinctive voice effect. Field studies using song types as playback have demonstrated that male song sparrows can discriminate between individual neighbouring males based on song types in their repertoires (Stoddard et al. 1991, 1992) even to the extent of recognition based on a single song type (Stoddard et al. 1991). Female song sparrows are responsive to structural differences in conspecific song (Searcy & Marler 1981; Searcy et al. 1985), and it is parsimonious to assume that females also have some ability to distinguish males by the song types in their repertoires. Although not conclusive, the above evidence supports the notion that female discrimination in the present study was based on recognition of song types that compose the repertoires of their mates.

Sexual preferences shown by female birds in response to playback of song may be important in the context of intra- versus extra-pair copulations (Searcy 1992b). These preferences are based solely on songs presented and are not confounded by other factors that might influence female choice of mate in the wild. Thus, solicitation experiments may mimic the circumstances surrounding many extra-pair copulations (Birkhead & Møller 1992; Searcy 1992b) and could provide clues to which vocal variables are likely to be significant to female extra-pair choice in nature. For example, Catchpole et al. (1986) showed that female great reed warblers, *Acrocephalus arundinaceus*, display more for large-syllable repertoires. A recent study of extra-pair paternity in great reed warblers in Sweden showed that all extra-pair fertilizations detected involved extra-pair males with larger repertoires than the social mates who were cuckolded (Hasselquist et al. 1996). To date, whether extra-pair paternity occurs in song sparrows is unknown. Results from the present study suggest that song types in a male's repertoire may influence the reproductive behaviour of female song sparrows. In future studies, we will investigate whether females discriminate between songs of males in neighbouring territories versus other non-mate male songs. In many species, neighbouring males are most likely to be responsible for extra-pair fertilizations (e.g. Hasselquist et al. 1996; Gray 1996).

In an apparently monogamous and highly vocal songbird such as the song sparrow, female recognition of her mate based, at least in part, on his singing behaviour is not unexpected (Falls 1982). Studies of other species have shown that individual recognition is feasible based on the extent of intraspecific variation in the structure of songs (Marler & Donald 1960; Rothstein & Fleischer 1987; Weary et al. 1990; Weisman et al. 1990; Ritchison 1991). It is more difficult to demonstrate that such recognition actually occurs in nature or that it is of some consequence in a reproductive context. The sexual responses of females to the songs of individual males shown in the present study seem to meet both of these criteria. It remains for future studies to determine the exact circumstances in which female recognition and preference for mate song may affect reproductive success.

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