DOES FEMALE CHOICE SELECT FOR MALE SONG REPERTOIRES? FEMALE CHOICE OF EXTRA-PAIR MATES AND MALE SONG CHARACTERISTICS IN THE SONG SPARROW

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Most of the oscine passerines, or songbirds, have complex song repertoires consisting of many different song or syllable types, and both the size of the song repertoire and the specific song types sung are thought to affect fitness. The hypotheses explaining these song features divide into two categories, based on two widely recognized functions of bird song: (1) territory defense and (2) mate attraction and stimulation. These two categories of hypotheses are distinguished by the mechanism they suggest for maintaining song features: intermale contests in the case of territorial defense, and female choice in the case of mate attraction.

That song repertoires affect male-male contest competion has been well established by field experiments ***e.g., (Krebs et al., 1978). However, female choice for elaborate song displays has been harder to document. Laboratory studies using copulation solicitation displays have documented that females are able to discriminate different features of male song repertoires, but how these laboratory preferences translate to the field is not always clear. In the example of the sedge warbler, *Acrocephalus schoenobaenus*, laboratory preferences by females for large repertoires have been confirmed in the field: males with large repertoires attract mates sooner (Catchpole, 1980; Catchpole et al., 1984). But in other species, such as the song sparrow, *Melospiza melodia*, clear preferences shown in the laboratory do not appear to influence pairing date or speed of attracting a replacement female after mate removal in the field (Searcy, 1984; Searcy and Marler, 1984). In field studies, experimenters' ability to measure female preference for songs faces a major confound: female preferences for male attributes such as song repertoire may be overridden by the need to choose a better territory.

Perhaps the most promising area of research for uncoupling the confounding influences on female choice in the field is study of extra-pair mating behavior. Extra-pair mating is widespread: most socially monogamous songbirds engage in extra-pair copulations (Birkhead and Møller, 1995). Extra-pair copulations are generally thought to be under female control (Birkhead and Møller, 1992), and may thus be a good measure of female preference. In addition, female songbirds are thought to get no benefits from the territory of an extra-pair male ***with only rare exceptions; see(Gray, 1997), so females choosing extra-pair mates, possibly seeking "good genes," would be expected to discriminate on the basis of intrinsic male characteristics (such as song), not territory quality. The copulation solicitation assay, which effectively reveals female preferences in laboratory tests, is thought to mimic female solicitation of extra-pair copulations more than female choice of social mates (Searcy, 1992). Finally, extra-pair mating has important fitness consequences: extra-pair fertilizations increase variance in male reproductive success (Møller and Ninni, 1998; Webster et al., 1995; Yezerinac et al., 1995), so female choice for extra-pair mates may be an important selective force on male displays (Kose and Møller, 1999; Møller and Ninni, 1998; Møller and Tegelstroem, 1997).

Song sparrows as test subject

In many ways, song sparrows provide an excellent opportunity to test hypotheses about female choice for song characteristics. Song sparrows are drab, sexually monomorphic songbirds, but males are vigorous and persistent singers, so song is an obvious vocal "ornament" that females might assess. Song sparrow song has been well studied in the laboratory and field. Each male sparrow sings a repertoire of 5-13 songs, and song repertoires don't change with age (Cassidy, 1993; Nice, 1943). Males share a variable number of song-types with each neighbor ***reviewed in (Hill et al., 1999; Hughes et al., 1998).

There is also reason to think that female song sparrows might benefit by choosing males on the basis of their song repertoires. Song sparrow repertoire size correlates positively with survival (Hiebert et al., 1989). High levels of song sharing with neighbors have also been shown to correlate with survival in song sparrows, perhaps more than does repertoire (Beecher et al., 2000; Wilson et al., 2000). Both these findings suggest that song repertoires may accurately indicate male quality. In the laboratory, female song sparrows have shown the ability to recognize more than 60 individual song types (Stoddard et al., 1992). Female preference for large song repertoires has been demonstrated in the laboratory (Searcy, 1984), and females have also shown a preference for specific song types, especially those types most similar to those of their social mates (O'Loghlen and Beecher, 1997; O'Loghlen and Beecher, 1999). All these studies suggest that female song sparrows can, and perhaps should, discriminate between males based on song, although one study of pairing date failed to show a correlation with song repertoire size (Searcy, 1984). It has also been suggested that males may who share song types with their neighbors may be more likely to successfully solicit extra-pair copulations from the neighbor's mate, taking advantage of a female's preference for songs similar to her mates' (O'Loghlen and Beecher, 1999). Female preference for specific song types, or for shared songs in general, has yet to be tested in the wild.

Song features prominently in copulatory behavior in song sparrows. Males sing immediately prior to most within-pair copulations, and playback of recordings of neighbor or stranger song during a wild female's fertile period can stimulate her to give repeated precopulatory displays (pers. obs.), suggesting a possible role of song in extra-pair copulations. Recent research has also shown that a substantial proportion of song sparrow offspring derive from extra-pair fertilizations (Keller, 1996). I tested three hypotheses about the influence of song on female choice of extra-pair mates in song sparrows: (1) females should choose extra-pair males with large song repertoires; (2) females should choose extra-pair males who share many song types with their neighbors; and (3) females will be more likely to mate with an extra-pair male if he shares more songs with her social mate.

METHODS

Study site

Discovery Park, in Seattle, Washington, is an undeveloped wooded park, where Beecher and colleagues have conducted a long-term study of song sparrows since 1986 (Beecher et al., 1994). Song sparrow habitat, in the understory of deciduous and mixed woods, is nearly continuous at our study site, only occasionally interrupted by mowed fields. Song sparrows at Discovery Park are year-round residents. Territories are small (0.2-0.4 ha) and dense (30-40 per 10 ha).

Capturing adult sparrows

As part of an ongoing study of song sparrow behavior, sparrows in Discovery Park were captured in mist-nets and banded with a unique combination of metal (U.S.F.W.S) leg band and three colored plastic bands. Song sparrows that were adults in this study were generally banded as juveniles in their first summer or fall, or upon territory establishment in spring. A small blood sample (20-150 µl) was taken from each bird at the time of capture.

Delineating territories

I delineated territorial boundaries by observing the movements and singing patterns of banded birds. I also observed interactions between neighbors at territorial boundaries (Nice, 1943). Territory boundaries were marked onto small-scale maps.

Finding nests

In 1995 and 1996, I closely monitored five to ten song sparrow territories, and found most nests that fledged young in those territories. In 1997 and 1998, I monitored an area that included 35-40 territories, and found all the nests in those territories. I found most nests when the female was nest-building or incubating. In nests that survived to hatching, I visited the nest when chicks were seven days old to band chicks and take a blood sample from them. Song sparrow chicks usually fledge at ten days old, and achieve independence at about 30 days. I did not confirm that all banded chicks fledged; all measures of reproductive success reported hereafter are based on chicks reaching age seven days.

Recording songs

Male song sparrows sing discrete song types, and deliver them with what has been termed "eventual variety," usually repeating each song 5-20 times before switching to a new type. The modal repertoire size in this population is eight songs. Each male's song repertoire was recorded onto cassette tapes using Sennheiser ME-88 directional microphones and Sony TC-D5M tape recorders. A bird's repertoire was considered fully recorded if we recorded at least 15 consecutive switches between song types, or at least 20 switches if recording was not continuous. The average bird was recorded for >30 total switches. Tapes were analyzed on a Kay DSP 5500 sonograph. We printed sonograms of all song types, and all major variants of each song type.

Measuring song characteristics

Shared songs, defined as songs showing close similarity for 50-100% of their length, were identified from printed sonograms by consensus of three independent judges (see Figure 1 for examples). I calculated a sharing index between each pair of neighboring birds, equal to $2N_S/(R_1+R_2)$, where N_S is the number of shared songs and R_1 and R_2 are the repertoire sizes of the two birds (McGregor and Krebs, 1982). I also calculated for each male the average of his sharing indexes with all adjacent neighbors.

Genotyping

Upon collection, all blood samples were immediately stored in 750 µl lysis buffer (0.1M Tris-HCl pH8, 0.1M EDTA, 0.01M NaCl, 0.5% SDS). I stored samples in buffer at room temperature or 4°C for up to three years before DNA extraction, with no apparent degradation of the DNA.

I extracted DNA from samples with a standard phenol-chloroform extraction., followed by ethanol precipitation. I amplified seven microsatellite DNA loci for each sparrow. Four of these loci, Mme2, Mme7, Mme8 and Mme12, were developed from a song sparrow genomic library (K. Jeffery and L. Keller, pers. comm.). An additional locus, Psap335, was developed in Savannah sparrows (*Passercula sandwichensis princeps* ; M. Temple, M. Leonard and L. Hamilton, pers. comm.) and proved polymorphic in song sparrows. Two additional loci, Escµ1 and GF05, were developed in reed buntings (*Emberiza schoeniclus*) and medium ground finches (*Geospiza fortis*) respectively, and are also polymorphic in song sparrows (Hanotte et al., 1994; Petren, 1998). Amplifications (8 µl total volume) were carried out in 1X PCR reaction buffer (Promega), with 0.5mM dNTPs, 1.5-3.0 mM $MgCl_2$, with forward and reverse primers at 0.05-0.2mM and 0.3 units *Taq* polymerase. Forward primers were labeled with fluorescent tags. PCR products were separated using an automated DNA sequencer (ABI 373A, PE Biosystems, Inc.). I analyzed the results using GeneScan and Genotyper software (PE Biosystems, Inc.). Alleles were recognized based on differences in length. DNA from one bird was used as a positive control, and amplified and electrophoresed on each gel as a check on sizing accuracy.

Paternity exclusion power

I calculated paternity exclusion power, Q, for each of the seven loci, according to the formula in Weir (Weir, 1996). One locus, Mme7, is sex-linked in song sparrows, carried on the Z chromosome. Females are the heterogametic sex in birds, meaning that for Mme7, each female carries one allele and each male two. Females inherit Mme7 alleles only from their father, while males inherit alleles from both mother and father. Since each chick inherits an allele from its father, Mme7 should have comparable paternal exclusion power to an autosomal locus with the same allelic distribution in the population, and I applied the above formula to Mme7 as well. Given multiple independently assorting loci, the combined exclusion power is:

The ability of a set of loci to simultaneously exclude N males is given by

Paternity assignment

I assigned paternity by a two step process. First, as an error check, I compared a chick's genotype to that of its mother. If a chick mismatched its mother at a locus, the data for that locus were considered erroneous and discarded. If the chick matched the mother, that information was used to identify the chick's paternal alleles. The paternal alleles of the chick were then compared with the genotypes of all males in the population at the time the chick was hatched, and paternity was assigned by the criteria outlined below.

Paternity assignment criteria

The most common outcome was that one male matched the chick perfectly, and all other males in the population mismatched the chick at two or more loci. However, to correctly assign chicks despite genotyping errors and germ-line mutations (both rare; combined, these occurred in less than 4% of all comparisons) and occasionally incomplete data, I adopted the following criteria to classify chicks as either offspring of the social father or chicks resulting from an extra-pair fertilization, and to assign the correct genetic father to extra-pair chicks.

The social father was accepted as the genetic father if:

(1) The social father mismatched at no loci or one locus, all other males mismatched at more loci than the social father, *or*

(2) The social father mismatched at no loci or one locus, and the only other males that matched the chick as well as the social father were more than two territories away.

The social father was rejected if:

(1) The social father mismatched at two or more loci, *or*

(2) The social father mismatched at one locus and neighbor mismatched at none, providing that the social father was typed at five or fewer loci and neighbor typed at six or more, and there was no reason to suspect a genotyping error.

Paternity was considered equivocal, and chicks were excluded from further analyses, if:

(1) The social father mismatched at no loci, and a neighbor also mismatched at no loci, *or*

(2) The social father mismatched at one locus, and a neighbor also mismatched at one locus.

Once the social father was rejected, I accepted a male as genetic father if:

(1) He held a territory adjacent or one territory removed from the chick, he mismatched the chick at no locus, and was compared with the chick at four or more loci, and every other male within two territories mismatched at one or more loci, *or*

(2) He was a neighbor, mismatched a neighbor at only one locus, was compared with the chick at least six loci, and every other male within two territories mismatched at two or more loci.

<u>Correlations between singing behavior and extra-pair fertilization success</u>

There are several ways to evaluate "success" and "failure" in the competition for fertilization of a female's eggs. I compared social fathers who lost paternity in their own nest (cuckolds) with males who lost no paternity in their own nest, which is perhaps the simplest evaluation, but which has been commonly used in studies of extra-pair mating **e.g.(Møller and Ninni, 1998). Since I was able to determine the genetic (extra-pair) father in almost all cases, I also compared genetic fathers with the social father they cuckolded. Furthermore, since females consistently chose adjacent neighbors for extra-pair copulations, and occasionally chose more than one neighbor, it is reasonable to assume that females participating in extra-pair copulations evaluated and chose from among all adjacent neighbors. When females sample a limited number of mates, measured population-wide correlations between male trait and female choice are expected to be small, even if females are acting "choosy" (Benton and Evans, 1998). I therefore also compared genetic fathers and social fathers to their presumed competition, the set of all adjacent neighbors, using difference scores. This approach distinguished between female choice for a male with a repertoire of eight songs whose competitors all had repertoires of nine songs (difference score = -1 song), and for another male with eight songs whose neighbors instead had repertoires of six songs (difference score = +2). This technique is more powerful than simply comparing group means of chosen and unchosen males (Benton and Evans, 1998).

Statistical analyses

I computed averages weighted by chick. When calculating, for example, the average repertoire size of the genetic fathers of EPF chicks, a male who fathered three EPF offspring was weighted three times as heavily as a male who fathered only one EPF chick. For standard errors and statistical tests, however, the degrees of freedom reflect the number of males in each group, not the number of chicks. When comparing the characteristics of social or genetic fathers to the other potential fathers (defined as all immediate neighbors of the social father), I report difference scores; i.e., the amount by which the social or genetic father's trait differed from the neighborhood average.

RESULTS

Genotyping

Eighty-seven percent of birds were genotyped at six or more loci, 98% at five or more. On average, 6.4 loci per bird were available for paternity testing. In 3.6% of comparisons, mothers mismatched their chicks. Mismatches between chicks and social mothers can occur for three reasons: intraspecific nest parasitism (egg dumping), germ-line mutations, and genotyping errors. Intraspecific nest parasitism would typically result in chicks mismatching their social mothers at multiple loci, but matching the genetic mother at all loci. Social mothers and chicks that mismatched in my sample, however, usually mismatched at only one locus. Thus, these mismatches probably reflect a combination of genotyping errors and rare germ-line mutations (Primmer et al., 1996; Primmer et al., 1998).

Paternity exclusion power

Exclusion power for individual loci ranged from 0.28 to 0.82, averaging 0.66. Combined exclusion power of all seven loci was 0.9991. Using seven loci, the power to exclude four random males (a typical number of immediate neighbors) was 0.9946, and to exclude 12 males (which would exclude all males within two territories) was 0.9894. Power to exclude 40 males (the maximum number of males at the study site in any season) was still 0.9650. Power to exclude neighboring males when only six loci were available for comparison remained high: 0.9873 for four males, 0.9748 for 12, 0.9186 for 40. With only five of the seven loci available, power was over 90% for local neighborhood comparisons (0.9729 for four males, 0.9209 for 12), but dropped to 0.7598 if 40 males were considered as potential fathers.

Extra -pair mating

Forty-five of 191 chicks (24.0%) were the result of extra-pair fertilizations. For nine additional chicks, I had insufficient data to determine paternity unequivocally. Those chicks are not included in any of the subsequent analyses. Twenty-six of 75 nests (34.6%) had at least one extra-pair chick, and three nests (4.0%) had more than one extra-pair father. Due to the detected level of genotyping errors and germ-line mutations (as revealed by mother-chick mismatches), I first examined the 90 chicks for whom paternity was beyond question: those who perfectly matched only one male in the entire population, and who mismatched all other males at least 2 loci. Of these chicks, 20 were extra-pair. The genetic fathers of 19 of those 20 extra-pair chicks were adjacent neighbors to the social father; the twentieth father was a territorial male one territory removed from the social father. I used this spatial pattern of extra-pair paternity to create criteria for correctly assigning chicks to genetic fathers despite occasional mismatches between fathers and chicks, or occasional chance similarity of distant non-fathers and chicks (see Methods). Of the 45 extra-pair chicks, I was able to unambiguously assign paternity for 44. The one chick for whom I was not able to assign paternity was apparently fathered by a male from whom I had not obtained a blood sample, as the chick mismatched the social father and all neighbors at 3 or more loci, and mismatched all other males present in that year at 2 or more loci.

The proportion of chicks in the population that were due to EPFs did not vary significantly between years (range = 20%-30%, $\chi^2 = 4.88$, df = 3, P = 0.18), so I combined data from all years for further analyses. Furthermore, for males who were present in more than one year of the study, there was no correlation between their net gain or loss of paternity via EPFs in their first year and their second year (r = -0.016, df = 15, NS). I therefore considered a male's records of paternity in the two years to be independent.

Comparisons between song repertoires of cuckolded and non-cuckolded males

The song repertoires of cuckolded males did not differ from repertoires of males who reared at least one chick of their own but avoided being cuckolded (cuckolded males: 8.4 ± 0.4 songs; uncuckolded males: 8.8 ± 0.3; t = 0.45, df = 26, P = 0.65). The same held true when each social father was considered in the context of his local neighborhood. Cuckolded males had, on average, 0.10 ± 0.45 more songs in their repertoires than their immediate neighbors, while never-cuckolded males had 0.81 ± 0.46 more songs than their neighbors (t = 0.59, df = 26, P = 0.56).

Cuckolded males also did not differ from uncuckolded males in the extent to which their song repertoires overlapped with their neighbors, either when considered individually (average sharing index, cuckolded males: 17.1% ± 3.3%, never-cuckolded males, 14.7% ± 5.1%; t = 0.23, df = 26, P = 0.82), or when considered in the context of the local neighborhood (difference score = + 1.4 ± 2.4% vs. + 0.5 ± 2.2%, t = 0.17, df = 28, P = 0.87).

Pairwise comparisons between social and genetic fathers

Since I identified the genetic fathers of 44 extra-pair young, I was able to compare the characteristics of the social father and genetic father for each extra-pair chick. Genetic fathers did not differ from social fathers in repertoire size (8.4 ± 0.4 songs vs. 8.2 ± 0.4, respectively; t = 0.19, df = 28, P = 0.85) or in repertoire overlap (17.1± 3.2% of repertoire shared vs. 17.8 ± 3.7%; t = 0.09, df = 28, P = 0.93). The same held true (no difference between social and genetic fathers) when males were considered in the context of the immediate neighborhood of the social male (repertoire size difference scores: + 0.10 ± 0.45 vs. + 0.09 ± 0.47, t = .006, df = 28, P = 0.99; repertoire overlap difference scores: + 1.4 ± 2.3% vs. + 3.3 ± 2.8%, t = 0.33, df = 28, P = 0.74; social fathers first in all cases).

Sharing songs with the social fathers

There was no indication that the extent to which a potential EPF male shared songs with the female's social mate helped males gain EPFs: genetic fathers of EPF chicks shared on average 21.8 ± 6.5% of their repertoire with the social father. This was 2.1 ± 8.6% more than other neighbors of the social father, but the difference score did not differ significantly from zero (t = 0.28, df = 15, P = 0.79).

Net gain and loss of paternity via extra-pair fertilizations

The bottom line for any mating strategy is how it changes one's total contribution to the next generation. For that reason I calculated the net gain or loss of paternity through extra-pair fertilizations ("net extra-pair chicks") for each male in the population. Figure 2 plots net extra-pair chicks against song repertoire size for all males in the population, while Figure 3 plots the same only for those males involved in EPFs, either as a genetic father of EPF young or as a social father who raised the genetic offspring of another male. Figure 4, 5 and 6 plot net EPF chicks against a measure of song sharing, song repertoire overlap with neighboring males for all males, for males participating in EPFs and for the latter group of males with one outlier male removed. There was no significant correlation between repertoire size or song sharing and net gain or loss through extra-pair paternity (r=0.073, N=32, NS for all males, repertoire size, r = 0.20, N = 25, N.S. for all males, sharing; correlations similarly non-significant for subsamples of males in Figures 3,5, and 6). Figures 7 and 8 plot song repertoire size and song sharing, respectively, against total reproductive success of each male in the study: all extra-pair chicks plus all self-sired chicks raised in each male's own nest. Neither song variable correlates with total reproductive success.

DISCUSSION

In song sparrows, females do not appear to use song characteristics to choose extra-pair mates. Despite previous laboratory results suggesting that female song sparrows find larger repertoires more stimulating, the males who fertilized extra-pair young in this study did not have larger repertoires than the males they cuckolded, nor did extra-pair males have larger repertoires than their "competition," the other immediate neighbors that females could have chosen. Furthermore, despite laboratory results suggesting that females prefer songs similar to those of their own social mates, males successful at gaining extra-pair fertilizations in this study had song repertoires no more similar to the female's social mate than an average neighbor did. Recent field studies have shown a correlation between the degree to which a male song sparrow shares songs with its neighbors and that male's survival prospects. This suggests that high song sharing correlates with this measure of male quality. But females in this study did not choose extra-pair males who shared more songs with neighbors. For males who were involved in extra-pair mating, either by gaining an extra-pair fertilization or by rearing a chick fathered by another male, or both, there was no correlation between any aspect of male song repertoires and net gain or loss of paternity through extra-pair mating.

Taken together with a previous study on song sparrows that failed to find evidence for female choice of social mates by song repertoire size (Searcy, 1984), these data strongly suggest that the details of song repertoires do not affect female choice in the field in this species. There are several possible explanations for this negative result. The first explanation is that females really do have a preference, but our methods were inadequate to reveal it. While this is impossible to disprove entirely, the large sample of birds in this study (45 extra-pair chicks in 26 nests involving 31 different males) and the concurrence of the results from the field study of pairing date (Searcy, 1984) suggest that if there any effect of female choice must be extremely small.

It is also possible that the field results disagree with laboratory results concerning female choice in song sparrows because the laboratory paradigm is somehow misleading. Perhaps playback of an artificial repertoire of 16 songs through a loudspeaker is not interpreted by females as equivalent to hearing a male with 16 songs (such males don't exist in the wild). All non-song cues are controlled in the taped playback paradigm, but relevant social cues that give the experiment external validity may be eliminated as well. Laboratory preference tests using live male birds have formidable logistic difficulties, but have been used successfully for testing female preferences for visual displays (Hill, 1990). Perhaps such a test will be necessary to resolve the apparent paradox between laboratory and field results. Another interpretation of the contrast between laboratory and field results comes from considering that male traits need not necessarily match female preferences (Ryan and Rand, 1993). This hypothesis seems especially relevant since a preference for supernormal repertoire sizes has been observed in at least four species (Searcy and Marler, 1981; Searcy and Marler, 1984). Such a disparity, if real, could result from pre-existing sensory bias or from changes in female preferences lagging behind changes in male repertoire size, as may have happened in the case of the common grackle (Gray and Hagelin, 1996). Either way, mismatch between female preferences and male traits argues against explanations for song repertoires that center on coevolutionary, female-choice mechanisms such as good genes or runaway sexual selection.

If females do not exert strong preference for male song repertoires in the field, what does that tell us about the function of song in song sparrows? A muting experiment in another sparrow showed that males who were unable to sing at all apparently could not retain a female. Female seaside sparrows (*Ammodramus maritima*) appeared to ignore their own social mates as soon as the mates had been muted, even while those muted males still retained their territories (McDonald, 1989). But perhaps in some species, like the song sparrow, simply being able to produce song is sufficient for female attraction, and most of the observed complexity and flexibility in song repertoires is selected for only via male-male contest competition. While the dual function hypothesis of song function (that bird song's two functions are territory defense and female attraction/stimulation) seems widely applicable, the result of this study of song sparrow mating point out that the relative importance of the two functions may vary dramatically with the specific song traits examined. The relative importance of song to territory defense and female attraction may also vary widely between species, even among "conventional" socially monogamous territorial passerines.

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