

SONG REPERTOIRE SIZE AND MALE QUALITY IN SONG SPARROWS

WILLIAM A. SEARCY
PATRICK D. McARTHUR
AND
KEN YASUKAWA

ABSTRACT.—Female Song Sparrows (*Melospiza melodia*) perform more courtship display in response to large repertoires of song types than in response to small repertoires. This preferential response to large repertoires might be due to a positive correlation between repertoire size and male quality; therefore, females might benefit by responding more strongly to males singing many song types. We tested for such a correlation, using several measures of male quality. We found no evidence that repertoire size is related to male age, dominance status within captive flocks, territory size, date on which males settle on their territories, wing length, or weight. We suggest that adaptive explanations for the evolution of preference for large repertoires in this species are unsupported, and that this preference may be a phyletic holdover.

One set of explanations for the evolution of repertoires of redundant song types assumes that conspecific females show some type of preferential response to multiple song types (Krebs and Kroodsma 1980, Slater 1981). Such a preferential response could occur in mate choice or in reproductive activities after pairing. In Song Sparrows (*Melospiza melodia*), captive females perform more copulation solicitation display in response to multiple song types than in response to single song types (Searcy and Marler 1981). They continue to respond more strongly to larger repertoires across the entire range of repertoire sizes found among males of a study population (Searcy 1984). Solicitation display in Song Sparrows occurs, for the most part, well after pairing, and repertoire size appears to have no effect on mate choice (Searcy 1984). In other species, multiple song types have been shown to have a stimulatory effect on mate choice (Catchpole 1980), solicitation display (Searcy et al. 1982), and nest building (Kroodsma 1976). While these findings support the hypothesized advantage of repertoires for males, they concurrently raise another evolutionary question: why have females evolved preferential response to repertoires? Various authors have suggested that repertoire size is linked with some aspect of male quality. For example, it has been suggested that preferential response to large repertoires might be advantageous to females if males with large repertoires tended either to be older and more experienced (Catchpole 1980, Krebs and Kroodsma 1980), or to have better territories (Catchpole 1980) than males with small repertoires.

A second set of explanations for the evolution of repertoires assumes that repertoires function in territory defense (Krebs and Kroodsma 1980, Slater 1981). This possibility has not been investigated in Song Sparrows, but, in other species, experiments have demonstrated that multiple song types are more effective than single song types in excluding intruders from the territory (Krebs et al. 1978, Yasukawa 1981). Again, one possible explanation for these results is that repertoire size is correlated with male quality. For example, it has been suggested that non-territorial males might avoid territory owners with large repertoires because such males are either themselves large (McGregor et al. 1981), or are older and more experienced (Krebs and Kroodsma 1980, Yasukawa 1981).

We investigated the relationship between song repertoire size and various measures of male quality in Song Sparrows. Our first measure of male quality was age. Parental ability has been shown to increase with age in many species of birds (e.g., see Perrins and Moss 1974, Ryder 1980); therefore, male age is a logical measure of male quality—from the viewpoint of females. Success in aggressive encounters increases with age in some birds (e.g., Ketterson 1974, Searcy 1979); therefore, age of the territory owner is also a possible index of male quality—from the viewpoint of intruding males. Repertoire sizes are known to increase with age in some species (Nottebohm and Nottebohm 1978, Yasukawa et al. 1980), while they are known not to change with age in others (Dowsett-LeMaire 1981, McGregor et al. 1981). We tested for a relationship be-

tween age and repertoire size in Song Sparrows by determining whether repertoires of individual males increase in size from one year to the next.

Our second measure of male quality was aggressive dominance, measured as ability to defeat other males in encounters in flocks of captive birds. We assumed that a male's ability to defeat others in these flocks is positively correlated with his ability to defeat rivals when he is acquiring or defending a territory. This assumption is supported by Knapp and Krebs's (1976) demonstration that young male Song Sparrows that are successful in aggressive encounters in flocks are especially likely to be successful in claiming a territory. If this assumption is valid, then aggressive dominance is a logical measure of male quality from the viewpoint of intruding males. Females might benefit from responding preferentially to males of high aggressive dominance if such males tend either to own better territories or to be better at defending their mates from interference.

As a third measure of male quality, we used the quality of the territory owned by the male. Reproductive success of females in many species is affected by territory quality; female choice is often affected by territory quality as well (Searcy 1982). All else being equal, however, we can see no reason to expect intruding males to avoid good territories. We used two measures of territory quality: territory size and date of male settlement. Krebs (1977a) showed that repertoire size is correlated with territory size in the Great Tit (*Parus major*). Territory size has been shown to affect female choice in some species of birds (Verner 1964, Howard 1974, Nolan 1978), but not in others (Willson 1966, Holm 1973). Catchpole (1980) argued that the date when a male settles on a territory is a measure of territory quality because males should settle first on the best territories. In Song Sparrows, female preferences for mates have been shown to be correlated with date of male settlement (Searcy 1984).

Morphological measurements of size (i.e., wing length and weight) provided our final measures of male quality. Aggressive dominance increases with size in many animals (e.g., Collias 1943, Barnett 1963, Searcy 1979), so size is a possible measure of quality from the viewpoint of intruding males. McGregor et al. (1981) found no correlation between body size and repertoire size in Great Tits.

METHODS

Fieldwork was conducted at the Cary Arboretum of the New York Botanical Garden in Dutchess County, New York. Song Sparrows

held territories in riparian woodland, old fields, and marshes. In 1981 and 1982, we recorded males during March, April, and May. All but three males were caught and color-banded before being recorded; for the three males that were banded after being recorded, comparison of the recorded songs with those sung by the banded bird convinced us that the same individual was recorded and banded in each case.

Sound spectrograms were produced using a Princeton Applied Research Real Time Spectrum Analyzer, and then sorted into song types. In 1981, we estimated repertoire size by counting the number of distinct song types for any male for whom at least 200 renditions had been recorded. We occasionally found, however, an additional song type after the 200th song, so, for 1982, we raised our criterion and estimated repertoire size only for males for whom at least 300 renditions had been recorded.

We estimated repertoire size for 22 males in 1981 and for 20 in 1982. Morphological measurements were made when males were caught for color-banding. Wing length was measured to the nearest 0.5 mm as the length of the flattened wing. Males were weighed to the nearest 0.5 g using a 100-g Pesola scale.

Observations of singing males were plotted on large scale maps provided by the Cary Arboretum. Territory sizes were calculated as the areas of the smallest convex polygons containing all observations for individual males. We determined dates when males settled by censusing the study area for singing males at least three times per week, starting before any territorial males had settled on the area, and continuing until settlement ended.

We performed two experiments to examine the relationship between song repertoire size and dominance. In the first experiment, we determined both dominance and repertoire size in captive birds. In the second experiment, we determined repertoire size from field recordings, and then captured the males and determined dominance.

Subjects in Experiment 1 were 20 adult male Song Sparrows captured on their territories at scattered sites in Dutchess County late in the breeding season of 1981. The males were housed from August to October in individual cages; during this period, the subjects were able to hear each other, although they sang little or not at all. Early in October, they were assembled into four groups of five birds, and housed in outdoor aviaries. Each group was observed during October and November for 20 periods of 25 min. Focal animal sampling was used in recording displacements, fights, and chases. All birds were color-banded to allow individual

TABLE 1. Repertoire sizes of male Song Sparrows recorded in two successive years.

Male	Repertoire size in 1981	Number of recordings	Repertoire size in 1982	Number of recordings
1	8	247	8	300
2	9	209	9	300
3	9	335	9	300
4	9	295	9	300
5	9	118	9	300

identification of the winner and loser in each encounter.

In mid-November, the birds were moved back into the laboratory and housed in individual cages. Over the course of the next four months, we took them five at a time, treated them with implants of testosterone to induce singing, and placed them in individual sound attenuation chambers. Most males began singing one to three weeks after treatment. We usually recorded them for 1 h between 06:00 and 09:00, five days a week. Many of the birds initially sang highly variable "plastic" songs. These songs were ignored; only after songs were judged (by ear) to be crystallized were they transferred to edit tapes for analysis.

Sound spectrograms were produced for all

edit songs and then sorted into song types to determine repertoire sizes. Different codes were used for identifying males during the flock observations than those used during recording so that determination of repertoire sizes could not be biased by knowledge of dominance. In analyzing the spectrograms, we found that these laboratory-recorded songs were more variable than typical field-recorded songs. Furthermore, males in the laboratory usually sang each song type only once before switching to another, whereas males in the field usually repeated each song type many times before switching.

We based our estimates of repertoire sizes in the laboratory-recorded males on the first 30 bouts recorded for each male. A bout was simply defined as the consecutive repetitions of one song type. For six males, we did not obtain enough recordings to estimate repertoire size. In addition, one male died before his song was recorded. Thus, we obtained estimates of both aggressive dominance and repertoire size for 13 of the original 20 males.

We performed Experiment 2, in which field recordings of males were used to estimate repertoire sizes, because we could not be certain that the laboratory-recorded songs from Experiment 1 revealed natural repertoire sizes. In Experiment 2, we used as subjects, males

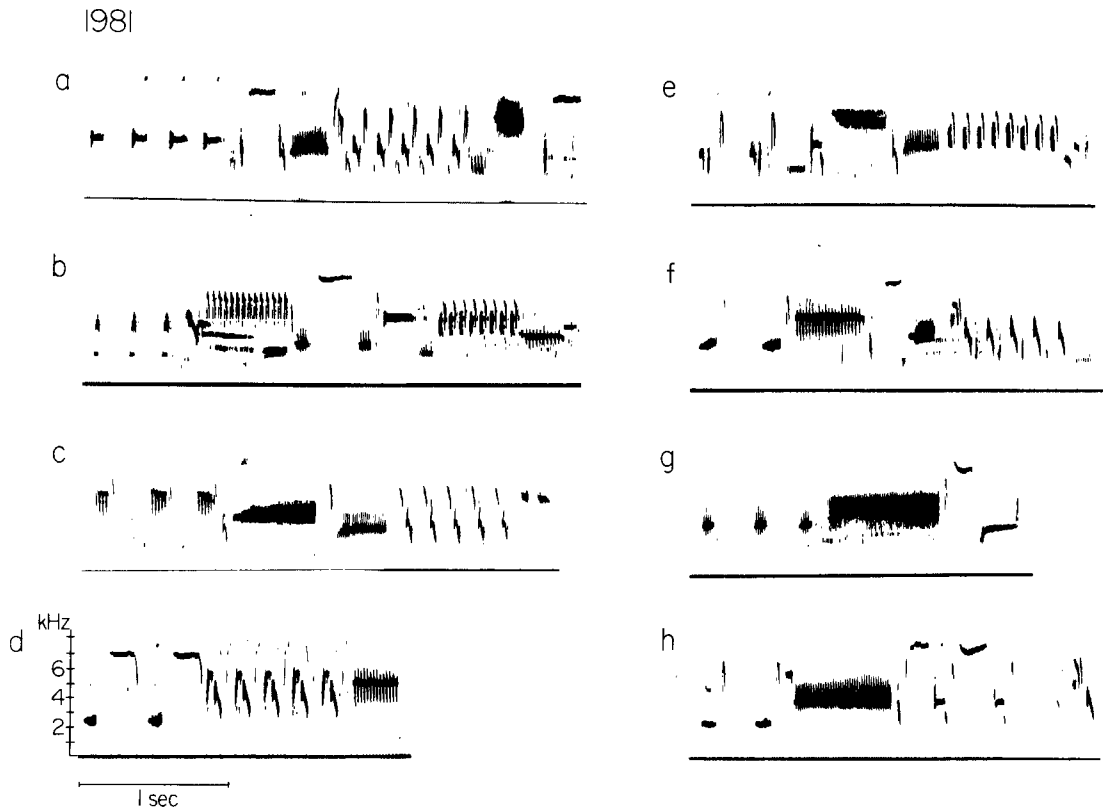


FIGURE 1. Sonograms of the repertoire of male 1 (Table 1) from 1981.

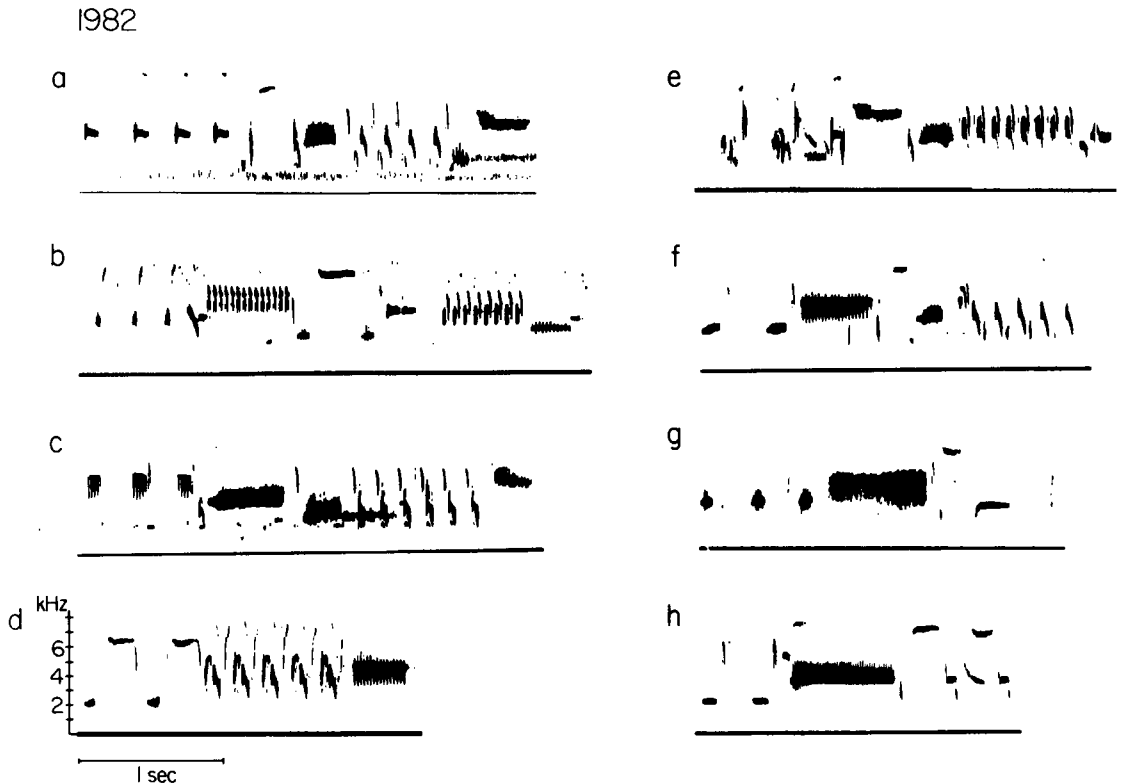


FIGURE 2. Sonograms of the repertoire of male 1 (Table 1) from 1982.

that we had previously recorded on their territories in 1982. The birds were captured in July, 1982 and held for 24 h in an outdoor aviary. Two groups of males were caught and observed, one of six and the other of five individuals. As in Experiment 1, we noted the identities of the winners and losers in all displacements, fights, and chases. Observations in Experiment 2 were made using ad lib sampling. The group of five males was observed for 9 h, and the group of six for 11 h.

Repertoire sizes for the birds in Experiment 2 were estimated by a person who had no knowledge of the outcome of the flock observations. For one of the 11 males, we had insufficient recordings to estimate repertoire size; therefore, we obtained estimates of dominance and repertoire size for 10 males.

Relationships between repertoire size and our indices of male quality were examined by calculating Spearman rank correlation coefficients. Statistical significance was accepted at the 0.05 level.

RESULTS

AGE AND REPERTOIRE SIZE

Five males were recorded in both 1981 and 1982. For four of these birds (1-4 in Table 1), we obtained enough recordings to meet our

criteria for estimating repertoire sizes in 1981 (200 songs) and in 1982 (300 songs). Repertoire sizes were identical in the two years for all four males. In addition, we obtained a sample of 118 recorded songs for a fifth male in 1981 (male 5 in Table 1). Although this sample was below our criterion for estimating repertoire sizes, we nevertheless found an equal number of song types in this small sample as in our 1982 sample of 300 songs. We conclude that for these five males, repertoire sizes did not change from one year to the next.

Nice (1943) provided repertoire sizes for two different years for two male Song Sparrows, based in each case on observations of many hundreds of songs. Her male 1M sang six song types in 1929 and six in 1930. Male 9M sang nine song types in 1929 and nine in 1935. Again, repertoire sizes did not change with age.

For the five males in Table 1, not only did repertoire sizes not change from year to year, but also each repertoire consisted of the same, individual song types each year. Nice (1943) reported that the same was true for the repertoires of her two males. As an example, Figure 1 shows the repertoire of male 1 in Table 1 as sung in 1981, while Figure 2 shows the corresponding song types for the same male in 1982. Not all the song types were absolutely identical in the two years. Song type "a" had

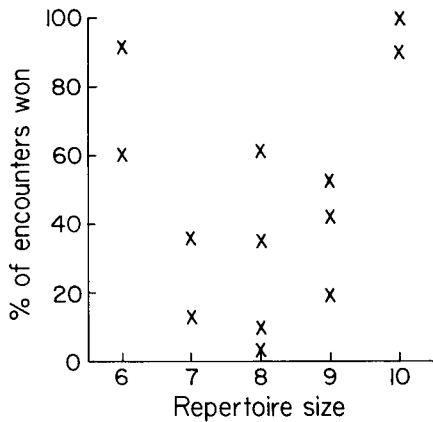


FIGURE 3. The relationship between song repertoire size (recorded in the laboratory) and percentage of encounters won in captive flocks for 13 male Song Sparrows (from Experiment 1). The relationship is not significant ($r_s = 0.186$, $P > 0.10$).

five syllables in the second trill in 1981 vs. four syllables in 1982, and the terminal notes differed slightly in the two years. Song type "h" also had slightly different endings in 1981 and 1982. Small changes such as these also occurred within years. Despite such changes, we had an overall impression of strong conservatism in the repertoire from year to year.

AGGRESSIVE DOMINANCE AND REPERTOIRE SIZE

In both of our experiments with captive flocks, well-defined dominance hierarchies were established. As one measure of aggressive dominance, we determined position in the hierarchy by constructing winner-loser matrices following the method of Brown (1975). The hierarchies determined in this way were all entirely linear, except for a single non-transi-

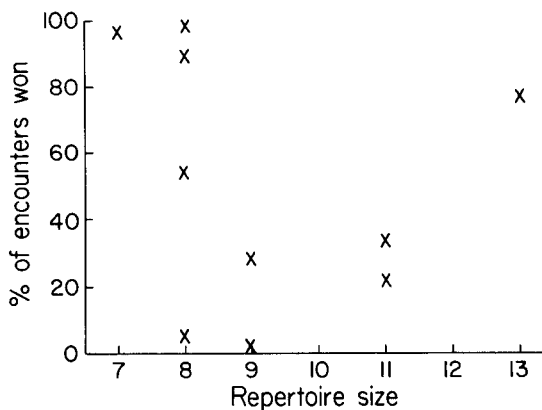


FIGURE 4. The relationship between song repertoire size (recorded in the field) and percentage of encounters won in captive flocks for 10 male Song Sparrows (from Experiment 2). The relationship is not significant ($r_s = -0.400$, $P > 0.10$).

TABLE 2. Spearman rank correlation coefficients relating Song Sparrow repertoire size and morphological measurements (sample sizes in parentheses).

Year	Wing length	Weight
1981	-0.099 (18)	-0.165 (15)
1982	-0.117 (19)	0.059 (18)

tive triad in one group in Experiment 1. We also calculated the percentage of all encounters that an individual won as a second estimate of dominance. The Spearman rank correlations between the two estimates of aggressive dominance ranged from +0.7 to +1.0; four of the five correlations were significant ($P < 0.05$). Since these two measures of dominance were so strongly correlated, the results of our subsequent analysis did not depend on which measure we used.

For the 13 laboratory-recorded males in Experiment 1, the correlation between repertoire size and percentage of encounters won was positive but non-significant ($r_s = 0.186$, $P > 0.10$; see Fig. 3). For the 10 field-recorded males of Experiment 2, the correlation between percentage of encounters won and repertoire size was negative but non-significant ($r_s = -0.400$, $P > 0.10$; see Fig. 4). We conclude that repertoire size is not related to aggressive dominance in Song Sparrows.

TERRITORY QUALITY AND REPERTOIRE SIZE

Territory size. For 22 males in 1981, we found no evidence of a correlation between territory size and repertoire size ($r_s = -0.228$, $P > 0.10$). For 15 males in 1982, we again found no significant correlation between territory size and repertoire size ($r_s = -0.214$, $P > 0.10$).

Date of male settlement. If territory quality is positively correlated with repertoire size, then repertoire size should be negatively correlated with date of male settlement, since the best territories should be occupied first. For 21 males in 1981, the correlation between repertoire size and date of settlement was positive though not significant ($r_s = 0.190$, $P > 0.10$). For 15 males in 1982, the correlation was negative but not significant ($r_s = -0.107$, $P > 0.10$). We conclude that repertoire size is not related to territory quality in Song Sparrows.

SIZE AND REPERTOIRE SIZE

We used two measures of overall body size, wing length and weight, neither of which was significantly correlated with repertoire size in either 1981 or 1982 (see Table 2). We conclude that repertoire size in Song Sparrows is not related to a male's body size.

DISCUSSION

We found no indication of a relationship between repertoire size and any of our measures of male quality in Song Sparrows. Repertoire sizes did not increase with age either in our sample of five males recorded in two years, or in Nice's (1943) sample of two males. Repertoire size was not correlated with aggressive dominance in either of two experiments with captive flocks. For each of two years of field observations, repertoire size was not correlated with measures of territory size and quality, nor with measures of male size. Although other measures of male quality may exist, we believe we have looked at, and eliminated, the most important ones.

If repertoire size is not an indicator of male quality, why then do females in laboratory experiments show a preferential response to large repertoires (Searcy and Marler 1981, Searcy 1984)? (We leave aside the question of why intruding males might avoid large repertoires, since such avoidance has not yet been demonstrated in Song Sparrows.) One possibility is that, in species in which males possess song repertoires, females have evolved heightened response to repertoires to facilitate species recognition; for example, female Song Sparrows might solicit more strongly for males with repertoires since all conspecific males possess repertoires and it is costly to copulate with a heterospecific individual. This hypothesis, however, does not explain why female Song Sparrows prefer increasingly larger repertoires within the range of repertoire sizes possessed by conspecific males. Furthermore, this hypothesis of species recognition predicts that in species in which males sing only one song type, females would respond more strongly to single song types than to repertoires. Females in such species, however, actually show no discrimination between single and multiple song types (Searcy and Marler 1984). A second possibility is that the female preference has evolved by runaway sexual selection (Catchpole 1980). Models of female choice predict that runaway selection will produce female preferences for traits that are otherwise non-adaptive or even maladaptive in males (e.g., O'Donald 1980, Lande 1981). One difficulty is that these models are meant to apply to situations involving choice of mates, whereas female choice of mates is not affected by repertoire size in Song Sparrows (Searcy 1984). It might be possible, however, to extend the models to cases in which females "choose" to be differentially stimulated by males after pairing. A second difficulty in applying these models to female response to repertoires is that the models require that

the male trait in question be heritable, since females benefit from responding to the trait only if their sons inherit the trait and its attendant attractiveness. Since song types are learned, repertoire size can be expected to have low heritability. In the only species for which data exist, the Great Tit, the father-son correlation of repertoire size is actually slightly negative (McGregor et al. 1981).

The remaining possibility is that female preferences for large repertoires are non-adaptive, the product of phyletic inertia (Gould and Lewontin 1979). Note that we are proposing only that the female response to repertoires is non-adaptive, and not that the repertoire itself is non-adaptive. The proximate mechanism that produces preferential response to repertoires is, at least in many cases, habituation (Krebs 1976, 1977b; Searcy et al. 1982). Thus, female Song Sparrows may solicit more often and more intensely in response to large, rather than to small, repertoires because several distinct song types are more effective in preventing habituation by females than one or a few song types. Krebs (1977b) argued that habituation can be altered by selection; however, we might expect, given the general prevalence of habituation throughout the vertebrates, that habituation will occur in the absence of selection against it. We suggest then, that preferential response to repertoires is a phyletic hold-over, with no real selective cost or benefit.

ACKNOWLEDGMENTS

We are grateful to the Cary Arboretum of the New York Botanical Garden for permission to use the study area. We thank Margaret H. Searcy, Nancy Masters, Virginia Sherman, Susan Peters, and James Mulligan for help in recording songs; Nancy Masters for help in classifying song types; and Margaret H. Searcy for drawing the figures.

LITERATURE CITED

- BARNETT, R. A. 1963. The rat: a study in behavior. Aldine, Chicago.
- BROWN, J. L. 1975. The evolution of behavior. W. W. Norton, New York.
- CATCHPOLE, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour* 74:149-166.
- COLLIAS, N. E. 1943. Statistical analysis of factors which make for success in initial encounters between hens. *Am. Nat.* 77:519-538.
- DOWSETT-LEMAIRE, F. 1981. Eco-ethological aspects of breeding in the Marsh Warbler, *Acrocephalus palustris*. *Terre Vie* 35:437-492.
- GOULD, S. J., AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. *Proc. R. Soc. Lond. B Biol. Sci.* 205:581-598.
- HOLM, C. H. 1973. Breeding sex ratio, territoriality, and reproductive success in the Red-winged Blackbird (*Agelaius phoeniceus*). *Ecology* 54:356-365.

- HOWARD, R. D. 1974. The influence of sexual selection and interspecific communication on Mockingbird song (*Mimus polyglottos*). *Evolution* 28:428-438.
- KETTERSON, E. D. 1974. Geographic variation in sex ratio among wintering Dark-eyed Juncos (*Junco hyemalis*). Ph.D. diss., Indiana Univ., Bloomington.
- KNAPTON, R. W., AND J. R. KREBS. 1976. Dominance hierarchies in winter Song Sparrows. *Condor* 78:567-569.
- KREBS, J. R. 1976. Habituation and song repertoires in the Great Tit. *Behav. Ecol. Sociobiol.* 1:215-227.
- KREBS, J. R. 1977a. Song and territory in the Great Tit, p. 46-62. *In* B. Stonehouse and C. M. Perrins [eds.], *Evolutionary ecology*. Macmillan, New York.
- KREBS, J. R. 1977b. The significance of song repertoires: the Beau Geste hypothesis. *Anim. Behav.* 25:475-478.
- KREBS, J. R., R. ASHCROFT, AND M. I. WEBBER. 1978. Song repertoires and territory defence. *Nature* 271: 539-542.
- KREBS, J. R., AND D. E. KROODSMA. 1980. Repertoires and geographical variation in bird song. *Adv. Study Behav.* 11:143-177.
- KROODSMA, D. E. 1976. Reproductive development in a female song bird: differential stimulation by quality of male song. *Science* 92:574-575.
- LANDE, R. 1981. Models of speciation by sexual selection on phenotypic traits. *Proc. Natl. Acad. Sci. U.S.A.* 78:3721-3725.
- MCGREGOR, P. K., J. R. KREBS, AND C. M. PERRINS. 1981. Song repertoires and lifetime reproductive success in the Great Tit (*Parus major*). *Am. Nat.* 118: 149-159.
- NICE, M. M. 1943. Studies in the life history of the Song Sparrow, part 2. *Trans. Linn. Soc. N.Y.* No. 6.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* No. 26.
- NOTTEBOHM, F., AND M. NOTTEBOHM. 1978. Relationship between song repertoire and age in the canary, *Serinus canarius*. *Z. Tierpsychol.* 46:298-305.
- O'DONALD, P. 1980. Genetic models of sexual selection. Cambridge Univ. Press, Cambridge.
- PERRINS, C. M., AND C. M. MOSS. 1974. Survival of young Great Tits in relation to age of female parent. *Ibis* 116:220-224.
- RYDER, J. P. 1980. The influence of age on the breeding biology of colonial nesting seabirds, p. 153-168. *In* J. Burger, B. Olla, H. E. Winn [eds.], *Behavior of marine animals: current perspectives in research*. Plenum Press, New York.
- SEARCY, W. A. 1979. Morphological correlates of dominance in captive male Red-winged Blackbirds. *Condor* 81:417-420.
- SEARCY, W. A. 1982. The evolutionary effects of mate selection. *Ann. Rev. Ecol. Syst.* 13:57-85.
- SEARCY, W. A. 1984. Song repertoire size and female preferences in Song Sparrows. *Behav. Ecol. Sociobiol.* 14:281-286.
- SEARCY, W. A., AND P. MARLER. 1981. A test for responsiveness to song structure and programming in female sparrows. *Science* 213:926-928.
- SEARCY, W. A., AND P. MARLER. 1984. Interspecific differences in the response of female birds to song repertoires. *Z. Tierpsychol.* 66:128-142.
- SEARCY, W. A., M. H. SEARCY, AND P. MARLER. 1982. The response of Swamp Sparrows (*Melospiza georgiana*) to acoustically distinct song types. *Behaviour* 80:70-83.
- SLATER, P. B. J. 1981. Chaffinch song repertoires: observations, experiments, and a discussion of their significance. *Z. Tierpsychol.* 56:1-24.
- VERNER, J. 1964. Evolution of polygyny in the Long-billed Marsh Wren. *Evolution* 18:252-261.
- WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. *Ecol. Monogr.* 36:51-77.
- YASUKAWA, K. 1981. Song repertoires in the Red-winged Blackbird (*Agelaius phoeniceus*): a test of the Beau Geste hypothesis. *Anim. Behav.* 29:114-125.
- YASUKAWA, K., J. L. BLANK, AND C. B. PATTERSON. 1980. Song repertoires and sexual selection in the Red-winged Blackbird. *Behav. Ecol. Sociobiol.* 7:233-238.

The Rockefeller University Field Research Center, Tyrrel Road, Millbrook, New York 12545. Present address of first author: Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260. Present address of second author: Department of Biology, Erskine College, Due West, South Carolina 29639. Present address of third author: Department of Biology, Beloit College, Beloit, Wisconsin 53511. Received 8 March 1984. Final acceptance 1 November 1984.