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SPARROW SEXUAL SIZE DIMORPHISM AND TESTIS SIZE:
A COMMENT

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Interspecific comparisons are most often used to test hypotheses regarding the evolution of sexual size dimorphism (e.g., Selander, 1966, 1972; Ralls, 1977; Searcy and Yasukawa, 1981). Recently, Rising (1987a) used an intraspecific approach in comparing the extent of dimorphism in samples of Savannah Sparrows (*Passerulus sandwichensis*) from many locations across their range. Among his results, one of great interest was the failure to support the prediction of the sexual-selection hypothesis that dimorphism should be more pronounced in polygynous than in monogamous populations. Elsewhere, using a similar approach and the same samples, Rising (1987b) failed to support the prediction that, due to increased mating opportunities, testes should be larger in polygynous than in monogamous populations (Cartar, 1985). Here, we argue that, because the critical assumption upon which both these results rely is tenuous at best, Rising's conclusions must be considered with great caution.

Sexual-selection theory attributes the increase in relative male size to the advantage that greater size provides in intrasexual competition for mates or for the resources necessary to attract mates. With the opportunity to attract more than one female (i.e., polygyny), competition becomes more intense, the payoff for winning increases, and thus, sexual size dimorphism is expected to become more pronounced. To test this prediction, ideally one would compare sexual dimorphism among species or among populations that vary in the degree to which they are polygynous. A much less powerful approach, and that used by Rising, is to compare sexual dimorphism in monogamous species or populations with sexual dimorphism in polygynous species or populations. In either case, knowledge of the mating system is critical.

Central to our argument is that the monogamy/polygyny dichotomy is artificial, since monogamy really represents one end of the polygyny continuum. Within a population, polygyny can range from less than 1% up to 100%, with the intensity of sexual selection predicted to vary accordingly. Verner and Willson (1969) defined polygynous species as having more than 5% of males regularly polygynous. Ford (1983) chose a value of 20% to separate facultatively polygynous species from regularly polygynous species. Therefore, to perform the tests reported by Rising (1987a, 1987b), it is necessary both to define the criterion for polygyny and to know the occurrence of polygyny in the populations being compared. In turn, knowledge of the degree of polygyny can only be obtained by studying the breeding biology of each population.

Rising (1987a) used samples from 11 "monogamous" and eight "polygynous" populations. Each sam-

pling location was assumed to represent a different population, in order that they could be considered as independent samples. However, the samples were not considered to be independent with regard to their mating systems, since all samples within the same general geographic region were assumed to have the same mating system. This assumption was necessary because the mating systems of only two of the eight polygynous populations and of only one of the 11 monogamous populations had been studied (Stobo and McLaren, 1975; Welsh, 1975; Weatherhead, 1979). Personal communications from researchers who had studied Savannah Sparrows at two other locations and had found them to be "almost always monogamous" (Rising, 1987b p. 65) were used to assign monogamous status to three populations sampled in the same region (e.g., the Canadian prairies) as the previous studies. Thus, the information critical to this analysis (i.e., the mating system) is assumed in 16 of the 19 samples used.

Is it reasonable to assume that mating systems remain constant across broad ecological or geographic areas? Probably not. For example, even on a local scale, Red-winged Blackbirds (*Agelaius phoeniceus*) consistently exhibit substantially different levels of polygyny in marsh and upland habitats (Eckert and Weatherhead, 1987). Also, within the same marsh study areas in eastern Ontario, mean harem sizes have declined from 2.80 in 1974 and 1975 ($N = 97$, Weatherhead and Robertson, 1977) to 1.91 ($N = 108$; Weatherhead, unpubl.) ten years later. The Savannah Sparrow populations sampled by Rising (1987a, 1987b) were often at substantial distances (e.g., up to 2,000 km) from the populations they were assumed to resemble in terms of mating systems and may have been sampled substantially later (given publication dates).

Rising (1987a, 1987b) argued that, at high latitudes, it is reasonable to assume that all populations are monogamous because Weatherhead (1979) found that the short breeding season favored monogamy. However, Weatherhead (1979) also found that the need for male parental care favored monogamy. If resources were sufficiently heterogeneous, eliminating the need for paternal care in the best habitats, one male could support two or more females simultaneously in spite of the short season, so all northern populations may not be monogamous. In the Canadian maritime region, Rising (1987a, 1987b) assumed that all populations are polygynous based on two studies (Welsh, 1975; Stobo and McLaren, 1975). However, no polygyny was found in a study of Savannah Sparrows in the upper St. Lawrence River valley adjacent to the maritime region (Bédard and LaPointe, 1984). Within the maritime region itself, in a study not addressing the mating system but

likely to detect polygyny (involving five years, 398 nests, 741 color banded adults and flying fledglings, and identified pairs), no mention of polygyny was made (Dixon, 1978). As Rising (1987b) suggests, this might indicate that his key assumption is incorrect. If we cannot be certain whether or not polygyny occurs or know the extent to which it occurs, then we cannot predict the intensity of sexual selection or its outcome.

We do not argue that Rising's (1987a, 1987b) results are wrong. Indeed, the sexual dimorphism result agreed in general with that reported by Weatherhead (1980) from a comparison of two populations of Savannah Sparrows with well-studied mating systems. However, because Rising's (1987a, 1987b) results rest on a questionable assumption, we do argue that his results cannot be accepted as correct. Thus, it remains to be determined whether Savannah Sparrows truly deviate from the predicted patterns of sexual size dimorphism and testis size.

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SEXUAL DIMORPHISM IN *PASSERCULUS SANDWICHENSIS* AS IT IS

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In two papers (Rising, 1987a, 1987b) I have used geographic variation among populations of Savannah Sparrows (*Passerculus sandwichensis*) to test predictions about the evolution of adaptations. In both, I have made certain assumptions about the breeding biology of birds from some populations that Weatherhead and Shutler (1989) feel were not justified. Al-

though I do not concur with their criticisms, they are, in any event, irrelevant.

The Savannah Sparrow is one of the most common North American songbirds. Perhaps due to this commonness, and because they are relatively easy to observe on their nesting grounds, there have been many careful studies of their breeding biology, and in this