ON THE USE OF AVIAN MORTALITY PATTERNS TO TEST SEXUAL SELECTION THEORY

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ABSTRACT.—To test the hypothesis that reduced survival of large males limits the extent to which sexual selection can increase male size, we examined mortality patterns in Red-winged Blackbirds (*Agelaius phoeniceus*) subjected to a surfactant spray. Univariate comparisons of wing measurements did not support the predicted mortality patterns. Although principal component analysis revealed that mortality was nonrandom with respect to some morphological characters, there was again no evidence of the predicted patterns either of directional selection favoring smaller males or of stabilizing selection favoring intermediate-sized females. This result led us to recognize that, like previous authors, we had made the incorrect assumption that large males should be more vulnerable to all mortality factors rather than the correct interpretation of the theory, that differential mortality should be seen as the net effect of all mortality factors. Only two published data sets are appropriate for testing the hypothesis, and neither shows differential mortality amongst males on the basis of size. *Received 22 February 1983, accepted 14 September 1983.*

THE correlation between the degree of sexual size dimorphism in birds and the variance in mating success of males relative to females provides one of the main supports for sexual-selection theory (Darwin 1871; Selander 1972), although in some specific instances this correlation has not been found (e.g. Weatherhead 1980). The implication of the relationship is that larger size enhances an individual's ability to compete for mates. In considering what pressures constrain male size from getting even larger, Selander (1965) hypothesized that the enhanced mating ability of large individuals is balanced by their lower survival. Because females of most avian species are under weak sexual-selection pressure relative to males, their size should approximate the ecological optimum for individuals of that species, that is, the size that maximizes survival. In birds therefore, females can be considered a control group against which one can compare relative male survival to assess the extent to which sexual selection has moved males away from the ecological optimum for the species.

Searcy and Yasukawa (1981) have described two methods of testing Selander's (1965) hypothesis. The first is to compare male and female survival between species that occur along a sexual-dimorphism gradient. Using the family Icteridae, which includes species with varying degrees of sexual dimorphism, Searcy and Yasukawa (1981) found that the survival of males relative to females decreased as the degree of dimorphism, and thus sexual selection, became more pronounced. This result is in accordance with Selander's (1965) hypothesis.

The second approach to testing the hypothesis is to compare mortality patterns within species. If male size is above the survival optimum and female size approximates the survival optimum, several predictions regarding mortality patterns should be met. In males one should find higher mortality amongst larger individuals, resulting in directional selection toward the female phenotype. If females are at the optimum, one should find higher mortality amongst females both larger and smaller than the mean, resulting in a pattern of stabilizing selection around the mean. Searcy and Yasukawa (1981) cite several studies that have provided data suitable for testing at least one of the above predictions. In some cases the predictions were supported and in others they were

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not. Our aim in this paper is to report the results of a study similar in design to one cited as supporting the hypothesis of higher mortality amongst larger males (Baker and Fox 1978). We use the results of our study to develop the argument that the data from a number of the studies cited by Searcy and Yasukawa (1981) are actually inappropriate for testing the predictions regarding mortality patterns in sexually dimorphic species for which the dimorphism is a product of sexual selection. To use these data for that purpose constitutes a misinterpretation of Selander's (1965) hypothesis.

AN APPARENT TEST OF SELANDER'S HYPOTHESIS

Baker and Fox (1978) compared male Common Grackles (*Quiscalus quiscula*) killed in a roost sprayed with a surfactant (Lefebvre and Seubert 1974) with those surviving the spray and found survivors to be smaller than nonsurvivors. They argued that although mortality was artificially induced, the surfactant spray simulates conditions that would exist in a severe winter storm. Following the same reasoning, we compared Red-winged Blackbirds (*Agelaius phoeniceus*) mist-netted before and after a surfactant spray with those killed in the spray at a roost in southern Quebec.

Methods.—All specimens were collected from a mixed species "blackbird" roost near Beauharnois, Quebec (73°59', 45°15') in April 1980. Birds were aged and sexed according to plumage characteristics (Meanley and Bond 1970). Individuals entering the first spring were called second year (SY) and older individuals were called after second year (ASY). The samples from before (12 ASY ♂♂, 35 SY ♂♂, 7 ♀♀) and after (7 ASY ♂♂, 26 SY ♂♂, 17 ♀♀) the surfactant application were collected during the periods 27 March–2 April and 16–21 April, respectively, by mist-netting birds as they entered the roost in the evening (for more details, see Weatherhead and Greenwood 1981). Birds that died following the surfactant application (11 ASY ♂♂, 12 SY ♂♂, 23 ♀♀) on 8 April were collected the following morning by walking transects through the roost and removing all dead birds within 0.5 m of the transect. Earlier surveys of the roost had indicated that there was very little natural mortality that produced a buildup of carcasses in the roost, and we were confident, therefore, that all dead birds collected following the spray had died as a result of the spray. The estimate of total mortality in the 150,000-bird roost resulting from the surfactant application was between 7 and 40%, with the uncertainty arising from the inability to census accurately birds that died away from the roost. Details of the surfactant application technique are available in Weatherhead et al. (1980).

Eleven morphological characters of the birds were measured. Weight was not used, because it is not a fixed structural character and because the surfactant birds may have lost weight before dying, as the cause of death is hypothermia. Similarly, feather measurements were avoided in case the surfactant caused changes in feather morphology that could bias the results. The data were subjected to principal component analysis to derive orthogonal factors from the original characters of all individuals within each age/sex cohort. Differences between groups within cohorts along each factor were determined using the Kruskal-Wallis test, while pairwise differences between groups were determined using median tests (Siegel 1956). The specific hypotheses to be tested were that: (a) larger males should be over-represented amongst the surfactant birds, and (b) extreme female phenotypes should be over-represented amongst the surfactant birds.

Results.—Wing length is generally considered the best indicator of body size in birds (Hamilton 1961, James 1970, Searcy 1979a). A univariate comparison of the two wing measurements between the different treatment groups provides little support for the predicted mortality patterns (Table 1). For ASY males, *t*-test comparisons of means of surfactant birds with before and after birds show no differences in humerus measurements. Mean ulna length of surfactant birds was significantly greater than before birds ($t = 2.13$, $P < 0.05$), in keeping with the predicted pattern, but no difference was found between surfactant and after birds. Among SY males no significant differences between surfactant and before and after birds were found for either wing character. Amongst females there was no evidence of increased variance about the mean of the wing measurements of surfactant birds (*F*-tests, $P > 0.05$) that would be expected were extreme phenotypes represented in that group. Overall, therefore, these univariate comparisons do not support the predictions of Selander's (1965) hypothesis.

The first three factors from the principal component analysis for ASY males collectively explained 61.7% of the variation (Table 2). Factor 2 should be a general indicator of body size based on the loading of wing measurements. The only factor on which the three groups differed significantly, however, was the third ($\chi^2 = 6.81$, $P = 0.033$). Seven of 11 characters

TABLE 1. Mean (± SD) lengths (mm) of the humerus and ulna of each treatment group by cohort.

	Before	Surfactant	After
ASY males			
Humerus	28.61 ± 0.55	28.82 ± 0.48	29.21 ± 0.87
Ulna	33.68 ± 0.69	34.44 ± 1.01	34.41 ± 1.13
SY males			
Humerus	28.75 ± 0.69	28.64 ± 0.75	28.73 ± 0.54
Ulna	34.34 ± 0.85	34.05 ± 0.93	34.16 ± 0.65
Females			
Humerus	24.49 ± 0.53	24.44 ± 0.50	24.53 ± 0.59
Ulna	28.62 ± 0.71	28.67 ± 0.88	28.51 ± 0.76

loaded significantly on factor 3, the two tarsus measurements being most prominent, followed by head width. A median test confirmed that surfactant birds had significantly higher scores on factor 3 than did before birds ($\chi^2 = 5.01$, $P = 0.025$). Condensed, these results indicate that, although the birds killed in the surfactant application differed slightly from those in the other two groups, those differences did not reflect the predicted vulnerability of larger individuals.

For the SY male data, the principal component analysis accounted for 60.0% of the variation over the first three factors (Table 3). As with ASY males, no separation of groups was found along the body size factor (factor 1), although the three groups differed significantly on the third factor ($\chi^2 = 7.44$, $P = 0.02$). Factor 3 is characterized by positive loadings of culmen length and depth and head-bill length. Significant pairwise differences on factor 3 were found between before and after birds ($\chi^2 = 11.1$, $P < 0.001$) and between before and surfactant birds ($\chi^2 = 3.9$, $P < 0.05$). Interpreting these results is difficult, because both perishing and surviving birds were characterized by longer heads and longer and deeper bills than the birds sampled before the spray. Considering only before and surfactant birds and comparing trends in SY males with those in ASY males also produces ambiguity. Of the common characters affected, large heads appeared to be disadvantageous in both groups, while culmen depth was affected in the two groups in an opposing fashion. What was consistent between both groups of males was the lack of evidence of any selective mortality on the basis of body size.

Principal component analysis of the female data accounted for 65.4% of the variation with the first three factors (Table 4). Based on the loading of wing measurements, factor 1 reflects variation in body size. Significant differences occurred between the three groups only on factor 2, however ($\chi^2 = 7.2$, $P = 0.027$), although median tests indicated no significant pairwise differences. Factor 2 was characterized as primarily one of head and culmen dimensions, with tibiotarsus length being represented to a lesser extent. For females, selection appeared to act against individuals with small heads, short and narrow culmens, and short tibiotarsi. As with males, however, this selection did not involve the factor reflecting body size.

Interpretation of the data.—The results of this study clearly do not support the Selander (1965) hypothesis. Although the data for both male age classes indicate that mortality may have been slightly selective in some instances, for neither age class was a survival advantage for smaller males demonstrated. The data for females showed a clearer case of selective mortality, but in a directional rather than a stabilizing pattern and involving a factor other than that reflecting body size. For a species as sexually dimorphic as the Red-winged Blackbird these results are rather surprising, particularly given Searcy and Yasukawa's (1981) data supporting Selander's hypothesis.

Several interpretations of these results are possible. It could be argued that the failure of the data to support the hypothesis was due to small sample size, although using only 16 surviving birds, Baker and Fox (1978) obtained results supporting the hypothesis. We feel there is a more fundamental problem with the data, however, and one that we recognized only as a consequence of obtaining results inconsistent with expectations.

In hypothesizing that mortality patterns resulting from a single mortality factor (thermal

TABLE 2. Character loadings from the correlation matrix on the first three principal components of variation in the data set for ASY male Red-winged Blackbirds.[a]

Character	Component of variance[b]		
	I	II	III
Head-bill length	0.850	0.101	0.389
Head width	0.078	0.248	0.455
Keel length	−0.079	0.818	−0.222
Humerus length	0.327	0.708	0.430
Femur length	0.622	0.053	0.129
Tibiotarsus length	0.331	0.644	0.484
Culmen length	0.834	0.221	0.077
Culmen width	0.418	0.085	0.169
Culmen depth	0.617	0.348	−0.365
Ulna length	0.261	0.708	0.367
Metatarsus length	0.121	−0.034	0.792

[a] Loadings are significant at $P = 0.05$ when larger than 0.361.

[b] Percentage of variance accounted for by component I = 38.0; component II = 12.4; component III = 11.3.

TABLE 3. Character loadings from the correlation matrix on the first three principal components of variation in the data set for SY male Red-winged Blackbirds.[a]

Character	Component of variance[b]		
	I	II	III
Head-bill length	0.304	0.411	0.490
Head width	−0.078	0.734	−0.001
Keel length	0.314	0.219	0.193
Humerus length	0.873	−0.117	0.133
Femur length	0.901	0.036	0.065
Tibiotarsus length	0.771	−0.023	0.109
Culmen length	−0.079	−0.180	0.851
Culmen width	0.053	0.730	−0.117
Culmen depth	0.029	0.515	−0.416
Ulna length	0.845	0.100	0.035
Metatarsus length	0.720	−0.263	−0.291

[a] Loadings are significant at $P = 0.05$ when larger than 0.209.

[b] Percentage of variance accounted for by component I = 33.7; component II = 14.8; component III = 11.5.

stress) at a single moment in time should be in accordance with Selander's (1965) hypothesis, we made an unwarranted assumption, albeit one that already appears in the literature. If increased size in males reduces survival ability, this should be reflected in their vulnerability to the *net* effects of *all* mortality factors. There is no reason to assume that large size should render a male more vulnerable to every mortality factor. On the contrary, large size may actually be advantageous in some circumstances, in spite of its contributing to higher net mortality.

The argument above is perhaps best illustrated using the specific example of Red-winged Blackbirds and a single incident of thermal stress. In general, the factors most likely to be of importance in surviving thermal stress will be the extent of fat reserves and the ability to minimize heat loss. The latter factor will presumably be reflected through surface-to-volume ratios, with larger individuals best suited to minimizing heat loss. The reason one cannot predict mortality patterns purely from the physics of heat loss, however, stems from the interaction of body parameters with the accumulation of fat reserves. It is known that the food habits of Red-winged Blackbirds change dramatically within a year in one location and that male and female diets can differ sharply from each other (McNicol et al. 1982). Thus, at any moment in time, the set of characters most efficient at exploiting the available food may best survive cold stress (due to superior fat reserves) in spite of not being best able to minimize heat loss. Because of dietary differences between males and females, the effect of cold stress at any moment in time may give an advantage to character sets that differ substantially between the sexes. Furthermore, as long as one character set is not best able to exploit all food types, then the same selection pressure may have quite different results within the same sex at different times of the year (e.g. cold stress in the fall, winter, or spring). Thus, it seems apparent that considerably more information than just the extent of sexual dimorphism in a species is required to make predictions about the mortality patterns expected from a single factor at a single moment in time. Recently, Boag and Grant (1981) provided an excellent example of how knowledge of the nature of the selection pressure, the ecology of the species, and the morphological characters relevant to both can lead to accurate predictions of mortality patterns.

OTHER TESTS OF SELANDER'S HYPOTHESIS

Unless one knows that mortality in a particular species is attributable almost entirely to a single factor, a seemingly unlikely possibility, then one must compare mortality over the range

TABLE 4. Character loadings from the correlation-matrix on the first three principal components of variation in the data set for female Red-winged Blackbirds.[a]

Character	Component of variance[b] I	II	III
Head-bill length	0.181	0.819	−0.013
Head width	0.173	0.502	0.078
Keel length	0.035	−0.079	0.898
Humerus length	0.883	0.023	0.032
Femur length	0.681	0.116	0.085
Tibiotarsus length	0.839	0.310	−0.005
Culmen length	−0.125	0.696	0.338
Culmen width	0.042	0.689	0.113
Culmen depth	0.043	0.104	0.867
Ulna length	0.846	−0.032	0.029
Metatarsus length	0.839	0.152	0.096

[a] Loadings are significant at $P = 0.05$ when larger than 0.287.

[b] Percentage of variance accounted for by component I = 33.9; component II = 17.6; component III = 13.9.

of normal mortality factors to determine the survival merits of different phenotypes. Ideally, one should follow the survival of a group of individuals from the time they hatch until all have died, as size differences may promote differential survival at any or all stages of life. For practical purposes, however, it seems reasonable to make comparisons of survivorship over a period of time sufficiently long to enable comparisons of individuals that will have been exposed to most events that could be associated with mortality (e.g. fall and spring migration, reproduction, thermal stress, predators, etc.).

What data, fulfilling the above criteria, are available that allow a comparison of mortality relative to size within sexes of a sexually dimorphic species? Of the five data sets cited by Searcy and Yasukawa (1981) as providing tests of the hypothesis that large males have lower survival than small males, three do not meet the criteria. As with the data in the present study, the data of Baker and Fox (1978) were collected from a single mortality event. The data of Johnson et al. (1980) for Brown-headed Cowbirds (*Molothrus ater*) and Red-winged Blackbirds are somewhat better, having been collected over two winter roosting periods, but the time frame is still too short to include events like migration and reproduction that may contribute significantly to mortality. In addition, their data for live birds were collected from decoy-trapped individuals and may be subject to bias (Weatherhead and Greenwood 1981). Although Johnson et al. (1980) were aware of the potential for bias, they were unable to correct for it. We should make one point clear. Our criticism of the above studies is only that their mortality data are inappropriate for testing Selander's (1965) hypothesis and not that they are inappropriate for other purposes.

Two studies cited by Searcy and Yasukawa (1981) compared mortality relative to size in males of sexually dimorphic species over a period of approximately a year, and these data should be appropriate for testing Selander's (1965) hypothesis. Searcy (1979a and b, respectively) compared sizes of returning and nonreturning male Red-winged Blackbirds and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) from one breeding season to the next. In both cases no evidence of higher survival of smaller males was found. Thus, the two best data sets do not support the hypothesis. Unfortunately, no data were provided for female mortality relative to size in either study.

Because Searcy and Yasukawa's (1981) between-species comparison of male mortality supported Selander's (1965) hypothesis, the results of both of Searcy's (1979a, b) within-species tests seem initially surprising. In failing to support Selander's (1965) hypothesis, however, these results are consistent with Weatherhead's (1980) failure to find greater sexual dimorphism in a polygynous, island population of Savannah Sparrows (*Passerculus sandwichensis*) relative to a monogamous, mainland population. Clearly, improved and more extensive tests of Selander's (1965) hypothesis are required to determine whether or not the hypothesis is flawed and, if so, which of the recently suggested alternatives best explains the results. Amongst the alternatives is Lande's (1980) suggestion that, even if sexual size dimorphism evolves due to sexual selection, the resulting ecological displacement of the sexes may be secondarily favored by natural selection such that neither sex is disadvantaged by their size. Searcy (1979a) has suggested that sexual selection is self-limiting: males that become too large are less efficient at holding territories and attracting mates due to energetic constraints imposed by large size. Neither of these hypotheses would predict the highly directional mortality amongst males towards smaller size that follows from Selander's (1965) hypothesis. Searcy and Yasukawa (1981) have also suggested that the higher relative mortality of males that they found among dimorphic species may not be due to selection against large size *per se* but against some attribute such as a behavioral dimorphism correlated with the interspecific size dimorphism. Because the correlation of the behavioral dimorphism with the size dimorphism need not necessarily hold intraspecifically, Searcy's (1979a, b) results would therefore not contradict those of Searcy and Yasukawa (1981).

In conclusion, there is an obvious need for further research to test the various hypotheses regarding the survival implications of sexual size dimorphism brought about by sexual selection. To be of value, however, it is imperative that those studies avoid the pitfalls identified in this paper.

ACKNOWLEDGMENTS

We are grateful to Ray Alisauskas and Roger Bider for their assistance with the surfactant applicant and collection of the surfactant-killed birds, to Bill Searcy, Brock Fenton, George Carmody, and several anonymous reviewers for their critical comments on earlier versions of the manuscript, and to Peter Boag for providing us with a prepublication copy of his manuscript with Peter Grant. Financial support was provided by Agriculture Canada and le Ministere de l'Agriculture du Quebec and through a Natural Sciences and Engineering Research Council of Canada operating grant to Patrick Weatherhead. Personal support to Hamilton Greenwood was provided by scholarships from the Natural Sciences and Engineering Research Council of Canada, the Fonds FCAC, and McGill University, and to Robert Clark by scholarships from the Fonds FCAC and McGill University.

LITERATURE CITED

BAKER, M. C., & S. F. FOX. 1978. Differential survival in Common Grackles sprayed with turgitol. Amer. Natur. 112: 675-682.

BOAG, P. T., & P. R. GRANT. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. Science 214: 82-85.

DARWIN, C. 1871. The descent of man, and selection in relation to sex. London, John Murray.

HAMILTON, T. H. 1961. The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. Evolution 15: 180-195.

JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51: 365-390.

JOHNSON, D. M., G. L. STEWART, M. CORLEY, R. GHRIST, J. HAGNER, A. KETTERER, B. MCDONNEL, W. NEWSOM, E. OWEN, & P. SAMUELS. 1980. Brown-headed Cowbird (*Molothrus ater*) mortality in an urban roost. Auk 97: 299-320.

LANDE, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. Evolution 34: 292-305.

LEFEBVRE, P. W., & J. L. SEUBERT. 1974. Surfactants as blackbird stressing agents. Proc. Vertebrate Pest Control Conf. 6: 156-161.

MCNICOL, D. K., R. J. ROBERTSON, & P. J. WEATHERHEAD. 1982. Seasonal, habitat and sex-specific food habits of Red-winged Blackbirds: implications for agriculture. Can. J. Zool. 60: 3282-3289.

MEANLEY, B., & G. M. BOND. 1970. Fall moults and plumages of the Red-winged Blackbird with particular reference to the fall migration. Bird-Banding 41: 22-27.

SEARCY, W. A. 1979a. Sexual selection and body size in male Red-winged Blackbirds. Evolution 33: 649-661.

———. 1979b. Size and mortality in male Yellow-headed Blackbirds. Condor 81: 304-305.

———, & K. YASUKAWA. 1981. Sexual size dimorphism and survival of male and female blackbirds (Icteridae). Auk 98: 457-465.

SELANDER, R. K. 1965. On mating systems and sexual selection. Amer. Natur. 99: 129-141.

———. 1972. Sexual selection and dimorphism in birds. Pp. 180-230 *in* Sexual selection and the descent of man 1871-1971 (B. Campbell, Ed.). Chicago, Aldine.

SIEGEL, S. 1956. Nonparametic statistics for the behavioral sciences. New York, McGraw-Hill.

WEATHERHEAD, P. J. 1980. Sexual dimorphism in two Savannah Sparrow populations. Can. J. Zool. 58: 412-415.

———, & H. GREENWOOD. 1981. Age and condition bias of decoy-trapped birds. J. Field Ornithol. 52: 10-15.

———, J. R. BIDER, & R. G. CLARK. 1980. Surfactants and the management of Red-winged Blackbirds in Quebec. Phytoprotection 61: 39-47.