

tion are often concentrated in the facial region (Ficken and Ficken 1968). Apparent assortative mating for bill size has been found in Dunlins (*Calidris alpina*; Soikkeli 1966), Eurasian Oystercatchers (*Haematopus ostralegus*; Harris 1967), Herring Gulls (*Larus argentatus*; Harris and Jones 1969) and Snow Geese (*Chen caerulescens*; Ankney 1977). RSD in bill size is greater than RSD of other measurements in Falconiformes (Mueller and Meyer 1985) and Strigiformes (Mueller 1986). In all, the hypothesis of Jehl (1970) appears to be a more likely explanation for the evolution of RSD in shorebirds than the hypothesis of Jehl and Murray (1986).

The correlation between RSD in shorebirds and the incidence of aerial displays is undeniable, but it appears that the selection producing RSD was not primarily for aerial agility. Perhaps aerial displays also play a role in facilitating rapid pair formation by enabling females to find males but the decision of the females is made afterward, on the ground, where such characters as bill length can have an influence, and it is then that sexual selection works to produce RSD.

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Response: Evolution of Sexual Size Dimorphism

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Based on a detailed survey of shorebirds, we proposed a theory regarding the evolution of sexual size dimorphism (SSD) that seems generally applicable to birds and perhaps other animals (Jehl and Murray 1986). Mueller (1989) has challenged our view and proposed an alternative hypothesis, which he applied only to those shorebird species in which the females are larger than the males (reversed sexual size dimorphism—RSSD). Before responding to Mueller's comments, we briefly present our theory in order for the reader to appreciate and to evaluate the differences in our views.

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We assumed that the kind and frequency of various mating relationships (monogamy, polygyny, and polyandry) that occur within a population is a consequence of the ratio of the males available for breeding to females available for breeding and of their probabilities of future successful reproduction (Murray 1984, 1985). We superimposed on this theory the hypothesis that agile males that engaged in aerial acrobatic maneuvers were dominant over less agile males in territorial contests or were more attractive to females. Inasmuch as smaller size increases agility (Andersson and Norberg 1981), species in which males perform aerial acrobatics should exhibit RSSD. Our theory is hypothetico-deductive. Thus, given (1) a particular ratio of breeding males to total males, (2) the prevailing mating system, and (3) the occurrence or nonoccurrence of aerial acrobatic display in the primary displaying sex (usually the male), we pre-

dicted 12 categories relating mating systems and body size dimorphism (Jehl and Murray 1986). The available data limited us to testing only the predictions concerning the direction of SSD. We specifically examined SSD in shorebirds and other groups of birds known to have species with RSSD. The predicted pattern of mating system, territorial or courtship display (aerial acrobatic or not), and sexual size dimorphism (normal or reversed) was largely corroborated by examples drawn not only from the diverse suborder of shorebirds (Charadrii) but from birds in general (Jehl and Murray 1986).

Mueller (1989) did not criticize our stated assumptions, our logic in reaching our predictions, or the evidence used in our presentation. Instead he argued that if aerial agility strongly affected RSSD the dimorphism index of body mass (which is the factor affecting wing loading and aerial agility) should be greater than the dimorphism index of other features (e.g. bill length and tarsus length) that are unrelated to aerial agility. That idea would be tenable only if the intensity of selection on wing loading exceeded that on other sexually dimorphic characters, but this is not necessarily the case. Nevertheless, because bill length often shows the greatest sexual dimorphism (especially among scolopacids), Mueller rejects our theory and proposes that RSSD has been selected as a means of facilitating rapid pair formation, a hypothesis that he attributes to Jehl (1970). We find Mueller's interpretation unsatisfactory for several reasons.

(1) Although Jehl (1970) did hypothesize that greater bill size differences may promote rapid pair formation in the Stilt Sandpiper (*Calidris himantopus*) and Least Sandpiper (*Calidris minutilla*), he concluded "This study sheds no light on why females in the species studied are the larger sex" (Jehl 1970: 317). In incorrectly citing Jehl (1970) as the source for the hypothesis that RSSD is a means of promoting rapid pair formation, Mueller (1989) confused the evolution of *direction* and the evolution of *magnitude* of SSD, a distinction made by both Jehl (1970) and Jehl and Murray (1986).

(2) We certainly were aware of the variation in dimorphism ratios of the features we used in discussing the evolution of SSD in birds (see our figs. 3-5 and table 1). Furthermore, we showed that the variation of these ratios seems to be affected by the mating system (monogamous vs. polygamous), as shown in our figures 6-8. We pointed out that despite the variation in the ratios within a species, the *direction* of dimorphism is almost always the same (see our appendices I and II). We suggested further that the *magnitude* of dimorphism in a particular feature could be affected by factors other than agility, such as the ratio of breeding males to total males, the mating system (whether monogamous or polygamous), selection for rapid pair formation, or even, in some instances, selection for ecological efficiency. That many

birds show extreme dimorphism in bill length is not surprising because facial characters seem important in promoting sexual recognition (Ficken and Ficken 1968, Jehl 1970), as Mueller acknowledges.

(3) Mueller's hypothesis has the same flaw as hypotheses that propose that RSSD evolved as a means of promoting ecological efficiency of the members of a pair. Simply, it does not account for the *direction* of SSD. Rapid pair formation and ecological efficiency could be achieved by a difference between males and females, regardless of which sex is bigger (Jehl 1970, Power 1980, Jehl and Murray 1986). We believe that the failure to recognize the difference between the evolution of *direction* and the evolution of *magnitude* of SSD is primarily responsible for the prevailing confusion of hypotheses concerning the evolution of SSD in birds and other animals.

(4) Mueller makes no predictions from his hypothesis, making it difficult to test. Presumably, if one knows that a shorebird has RSSD, one could predict that it lives in a situation favoring rapid pair formation, such as in the arctic where breeding seasons are short. But, this does not explain normal SSD (males larger than females) in arctic regions (e.g. Buff-breasted Sandpiper [*Tryngites subruficollis*], Pectoral Sandpiper [*Calidris melanotos*]) or RSSD in tropical shorebirds (e.g. Painted Snipe [*Rostratula benghalensis*], jacanas [Jacanidae]), much less the RSSD among non-migratory tropical raptors (often mated for life), or RSSD in other groups (e.g. sulids, fregatids, skuas, hummingbirds), or the SSD found in so many other birds.

We believe our theory is a general one that accounts for the pattern of SSD among birds. Our predictions regarding the direction of SSD are largely borne out by the available evidence. Predictions regarding the magnitude of SSD are more tenuous because more factors affect the evolution of magnitude of SSD, and rigorous testing is precluded by the present lack of sufficient data.

In contrast, Mueller merely restates earlier findings regarding the proximate basis for mate selection in some taxa (e.g. Jehl 1970, Jehl and Murray 1986), without recognizing that mate selection based on size differences could evolve regardless of which sex is the larger. His hypothesis makes no predictions and does not provide a general explanation for the pattern of SSD in birds.

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The Study of Geographic Variation

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The study of geographic variation has occupied a prominent place in ornithology. Historically most students of geographic variation were motivated by taxonomic interests, primarily subspecies description. Recent analyses of geographic variation have considered various topics of evolutionary interest. Two assumptions of most evolutionary studies of geographic variation are that geographic differences represent local adaptation, and that geographic differentiation is a stage in the speciation process. How these topics are studied is not universally agreed upon. Rising's (1988a) review of my Fox Sparrow (*Passerella iliaca*) study (Zink 1986) permits consideration of contemporary approaches to the study and interpretation of geographic variation.

Adaptation.—My results suggested high gene flow and near genetic identity of 31 "populations" at 38 protein-coding loci. This does not assure genetic uniformity at other loci. It does suggest a panmictic population structure, whereas inferences from morphological patterns might indicate a highly substructured population. Furthermore, available evidence (summarized in Barrowclough et al. 1985) suggests that enzyme variation is consistent with predictions of the mutation-genetic drift model of neutral theory and therefore useful for estimating gene flow and population histories. Thus, observed enzyme variation appears nonadaptive, although this does not rule out selection at other loci. From the observations of high gene flow and genetic uniformity, and a lack of environmental-morphometric associations, I suggested that the degree of morphological differentiation might

not be a reliable guide to genetic differentiation even at loci influencing morphology; environmental induction was posed as a potential mechanism of morphological divergence. Without the genetic data I probably would have favored the traditional interpretation that adaptation (e.g. natural selection) must be responsible for geographic differences in morphometrics but I simply could not find the telling environmental correlations (see Gould and Lewontin 1979).

My conclusion that geographic patterns of morphological variation were not necessarily results of adaptation prompted Rising to conjure an image of neutralistic "euphoria." This caricature denigrates an important body of empirical and theoretical knowledge on the evolution of genes in populations. For too long we have accepted uncritically the assertion (which might be true) that adaptation alone causes geographic differentiation, without tests of alternatives (see Lande 1985, Lynch and Hill 1986). For example, Rising advocated analysis of Fox Sparrow (*Passerella iliaca*) foods, from which one might discover an adaptive reason for geographic patterns in bill size; I concur and have resampled several populations for gizzard contents (the original 600+ samples were discarded by an entomological colleague). On the breeding grounds adults feed mostly on insects; thus, one needs to sample in winter when they feed on seeds (see maps in Grinnell and Miller [1944] for suitable study sites). Several populations with differing bill sizes are syntopic in winter, lending doubt to the effect of food choice on the evolution of bill size differences among breeding populations. Associations between bill and seed sizes might reflect adaptation as Rising expects, but experiments are needed to document that such correlations arise and are maintained because of increased fitness for individ-

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