

## COMMENTARIES

### Aerial Agility and the Evolution of Reversed Sexual Dimorphism (RSD) in Shorebirds

HELMUT C. MUELLER<sup>1</sup>

Jehl and Murray (1986) have proposed that RSD has evolved in shorebirds (Charadrii and Scolopaci) as a result of selection for small size in males for agility in aerial displays. An increase in aerial agility can result from an isometric decrease in size (Andersson and Norberg 1981). In this case, RSD (the ratio of the average for males divided by that for females) would be equal for all structures and thus, for the measurements given in Murray and Jehl, RSD would be, mass = wing = culmen = tarsus. However, aerial agility is strongly influenced by wing loading and selection for aerial agility should thus favor an increase in RSD in mass more than wing. Selection of RSD of other structures should be neutral, with the result that, mass > culmen = tarsus > wing.

I compare below the relationships between RSD in these 4 measurements for the species listed in appendices I and II of Jehl and Murray (1986), using the Wilcoxon matched-pairs signed-ranks test (Siegel 1956). The mean is used where more than one sample of measurements is presented. I follow the convention of using the cube-root of mass for comparisons with the linear measurements of wing, culmen, and tarsus. A species is considered to show RSD if females are larger than males in one of the four measurements; all other species are considered as having "normal" (male larger) dimorphism. Murray and Jehl indicate that the mating system, as well as the kind of display, influences the kind and degree of dimorphism. Dividing the shorebirds into groups of species based on the kind of display and mating system results in inadequate sample sizes for most groups. Of the few remaining groups of species all but one contain both species with RSD and species with normal dimorphism in numbers sufficient to frustrate analysis.

Fortunately, the one group available for analysis is not only the largest (64 of the 143 species listed in appendix I of Jehl and Murray), not only the most homogenous (only one species shows normal dimorphism in all four measurements), but it is also the group most pertinent to the question of whether selection for aerial displays is the important factor in the evolution of RSD: monogamous species with males performing acrobatic aerial displays. In this group, the mean RSD (male/female) for wing is  $0.980 \pm 0.019$  SD (range 0.96–1.05); only 3 species show normal di-

morphism and 6 are monomorphic. The mean RSD for culmen is  $0.933 \pm 0.060$  (0.74–1.04); only 3 species show normal dimorphism and 4 are monomorphic. The mean RSD for tarsus is  $0.972 \pm 0.028$  (0.90–1.06); only 3 species show normal dimorphism and 9 are monomorphic. The mean RSD for mass is  $0.965 \pm 0.025$  (0.91–1.04); only 2 species show normal dimorphism and 2 are monomorphic. RSD in culmen is greater than RSD in wing in 54 species, the opposite is true in only 9 species and 3 species show a zero-value tie ( $T = 129$ ,  $P < 0.0001$ ; all  $P$  values given are two-tailed). RSD in culmen is greater than RSD in tarsus in 51 species, the opposite is true in only 7 species and 7 species show a zero-value tie ( $T = 108.5$ ,  $P < 0.0001$ ). RSD in culmen is greater than RSD in mass in 29 species, the opposite is true in only 11 species and 8 species show a zero-value tie ( $T = 138$ ,  $P < 0.0002$ ). RSD in mass is greater than RSD in wing in 34 species, the opposite is true in only 7 species and 7 species show a zero-value tie ( $T = 125$ ,  $P < 0.0001$ ). RSD in tarsus is greater than RSD in wing in 38 species, the opposite is true in only 17 species and 10 species show a zero-value tie ( $T = 406.5$ ,  $P < 0.003$ ). RSD in mass is greater than RSD in tarsus in 23 species, the opposite is true in 12 species and 12 species show a zero-value tie ( $T = 218$ ,  $P > 0.11$ ). The following ordination is indicated: culmen > mass = tarsus > wing. This differs considerably from that predicted for selection for aerial agility in males.

Shorter bills in males can hardly confer an aerodynamic advantage over females. I agree with Jehl and Murray that the bill is an important secondary sex character and that the RSD in this structure is not the result of selection for foraging differences between the sexes. Jehl (1970) found that new pairs of the Stilt Sandpiper (*Calidris himantopus*) and the Least Sandpiper (*Calidris minutilla*) formed earlier and more rapidly where males were small and females were large. Jehl suggests that differences in bill length between the sexes may be the most important factor in promoting rapid pair formation, but finds the evidence equivocal because the sexes differ more in bill length than in tarsus or wing length. If, as I suggest, differences in bill length have been selected for more than other structures, then bill length may be the primary factor in promoting rapid pair formation. Jehl notes that it is unlikely that the size difference is important in sex-recognition and suggests that it may act to facilitate behavioral dominance of one sex over another and that this may be a prerequisite for a stable pair bond.

Visual characters associated with sexual recogni-

<sup>1</sup> Department of Biology and Curriculum in Ecology, University of North Carolina, Chapel Hill, North Carolina 27599-3280 USA.

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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#### LITERATURE CITED

- ANDERSSON, M., & R. Å. NORBERG. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* 15: 105-130.
- ANKNEY, C. D. 1977. Male size and mate selection in Lesser Snow Geese. *Evol. Theor.* 3: 143-147.
- FICKEN, M. S., & R. W. FICKEN. 1968. Territorial relationships of Blue-winged Warblers, Golden-winged Warblers, and their hybrids. *Wilson Bull.* 80: 442-451.
- HARRIS, M. P. 1967. The biology of Oystercatchers *Haematopus ostralegus* on Skokholm Island, S. Wales. *Ibis* 109: 180-193.
- , & P. H. JONES. 1969. Sexual differences in measurements of Herring and Lesser Black-backed gulls. *British Birds* 62: 129-133.
- JEHL, J. R., JR. 1970. Sexual selection for size differences in two species of sandpipers. *Evolution* 24: 311-329.
- , & B. G. MURRAY JR. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. *Current Ornithol.* 3: 1-86.
- MUELLER, H. C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. *Wilson Bull.* 98: 387-406.
- , & K. MEYER. 1985. The evolution of reversed sexual dimorphism in size: a comparative analysis of the Falconiformes of the western Palearctic. *Current Ornithol.* 2: 65-101.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences.* New York, McGraw-Hill.
- SOIKKELI, N. 1966. On the variation in bill- and wing-length of the Dunlin (*Calidris alpina*) in Europe. *Bird Study* 13: 256-269.

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### Response: Evolution of Sexual Size Dimorphism

JOSEPH R. JEHL JR.<sup>1</sup> AND BERTRAM G. MURRAY JR.<sup>2</sup>

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.

<sup>1</sup> Sea World Research Institute, Hubbs Marine Research Center, 1700 South Shores Road, San Diego, California 92109 USA.

<sup>2</sup> Department of Biological Sciences, Rutgers University, New Brunswick, New Jersey 08903, USA.

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-