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Plumage Color Correlates with Body Size in the Ruff (*Philomachus pugnax*)

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The behavioral and plumage polymorphism in the Ruff (*Philomachus pugnax*) is well-known but not yet fully understood. Males develop an elaborate and conspicuous breeding plumage with enlarged neck-feathers (the ruff) and ear-tufts, both of which vary from black and brown to white (Selous 1906–1907, Søgaard Andersen 1948). This plumage polymorphism is correlated with a behavioral polymorphism. Dark males form territories on a lek (i.e. independents; van Rhijn 1973), either as "residents" or "marginals," while white males behave as satellites and do not defend territories of their own (e.g. Hogan Warburg 1966, van Rhijn 1973).

Male Ruffs are larger than females, a situation which is rare in the Scolopacidae (Jehl and Murray 1986: fig. 2). Furthermore, resident males have, on average, longer wings than marginal males which in turn have longer wings than satellites (van Rhijn 1983). Territorial males also weigh more than satellites (Dobriniski in Cramp 1983) and dark males have longer wings than white males (Gibson in van Rhijn 1983 and Cramp 1983). Body size (measured as wing length) also appears to determine status on the lek among territorial males (van Rhijn 1983). Because wing length may increase with age in waders (e.g. Pienkowski and Minton 1973), differences in wing length among color

types could be due to age differences, with darker, territorial males on average being older than satellites. However, plumage color did not change between years among males that returned to the same lek (Søgaard Andersen 1948), though male age was unknown in that study (all observations were based on adult birds only). Thus, plumage color, body size, and age may all be correlated and contribute to the mating tactics used by individual males.

Van Rhijn (1973, 1983) suggested that both the color and behavior of Ruff males were controlled genetically by separate but linked sets of genes, now at equilibrium. Reproductive success was thought to be the same for territorial males as for satellites. This may constitute an example of a mixed evolutionary stable strategy (mixed ESS; Maynard Smith and Parker 1976) where dark and light males are maintained in the population by equal genetic payoffs, though different costs and benefits are associated with the two strategies (Maynard Smith 1983).

We measured four body-size characters in ruff specimens in full breeding plumage from the collections of the British Museum in Tring, England, and the Natural History Museum in Stockholm, Sweden. One of these characters, tarsus length, is an age-independent character (Garnett 1981, Alatalo and Lundberg 1986) and should be a useful control for age differences between differently colored males. We measured bill (culmen) and tarsus (tibio-tarsus) length to

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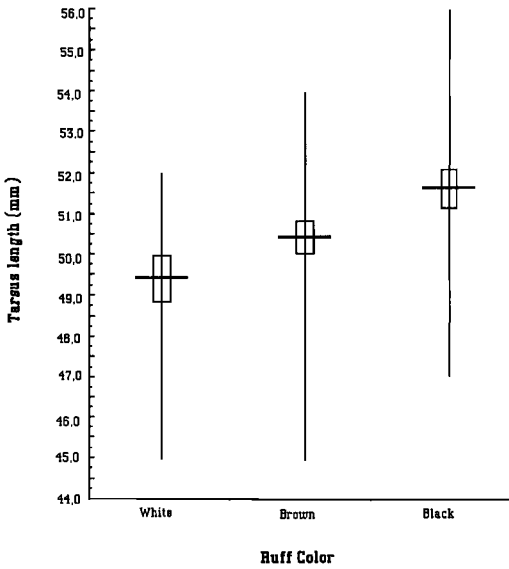


Fig. 1. Tarsus length (mm) vs. Ruff color. Horizontal bars indicate the mean for each color morph; boxes are ± 1 SE; and vertical bars show the range.

the nearest 0.1 mm with a digital caliper. Wing (flattened) and tail (longest tail feather) lengths were obtained to the nearest mm with a ruler. We measured only those specimens that could be classified clearly into 1 of 3 discrete plumage categories: black ($n = 16$), brown ($n = 23$), and white ($n = 20$). Speckled, dotted, or vermiculated birds, and birds with different colors on the ruff and ear-tufts were excluded because they could not be classified unambiguously. All measurements were taken by one person to reduce measurement error. Furthermore, only birds from Fennoscandia and the Soviet Union which is the main breeding range of the Ruff (Cramp 1983) were included.

We found that black males were the largest, brown

were intermediate, and white were the smallest in bill, tarsus, wing, and tail length. Black and brown males never differed significantly in size measurements. Brown and white birds were only significantly different in bill length whereas black and white were significantly different in all four characters (Table 1). The range of tarsus lengths (Fig. 1), and the overlap between measurements of differently colored males will be discussed below. Overall, we found that plumage color was correlated with body size, and probably behavior, such that the darker the secondary sexual characters (ruffs and tufts), the larger the bird. This corroborates earlier findings, but the differences in tarsus lengths also show that the larger size of darker birds is not simply an age effect.

The equal genetic payoff explanation (Maynard Smith 1983, van Rhijn 1983) is compatible with our finding that dark males were larger than white. The genes for large size could be coupled to behavior in the same way as the genes for plumage color. However, we suggest that the evolution and maintenance of the behavior, plumage and size polymorphisms of the Ruff can also be explained from nonequal payoffs for different color morphs. We propose that low-quality males (e.g. those growing up in poor feeding habitats or years) might be forced into satellite behavior during mating because of their smaller size. Size is a quantitative character controlled by many genes (Falconer 1981) but influenced by food conditions during growth (see Würdinger 1975, Ankney 1980 for examples from precocial birds), and it may determine the status of individuals (Fretwell 1969, Glase 1973). Thus small males may make the best of a bad situation by adopting a satellite mating strategy. Under this hypothesis one might expect all dark males to be larger than white, but we found a considerable overlap (Fig. 1). There are several reasons to expect a size overlap between color morphs. The most obvious in our case is that the sample was collected from a large geographic area. It is well-known that birds show considerable geographic variation in size (Zink and

TABLE 1. Mean \pm SD, lengths (mm) of bill, tarsus, wing, and tail of Ruffs in different color types. Sample sizes are given in parentheses and sizes were compared across color types with one-way ANOVAs. Lines join color types that are not significantly different (Scheffe's test, $P > 0.05$).

	Ornament color			ANOVA	
	Black	Brown	White	F	P
Bill	35.2 \pm 0.8 (13)	35.5 \pm 1.3 (21)	34.4 \pm 1.4 (18)	3.40	0.04
Tarsus	51.7 \pm 2.3 (16)	50.4 \pm 1.8 (23)	49.4 \pm 2.1 (20)	4.79	0.01
Wing	187.1 \pm 3.4 (15)	184.7 \pm 2.5 (23)	182.8 \pm 5.8 (20)	4.59	0.01
Tail	69.6 \pm 3.1 (16)	67.7 \pm 3.2 (21)	66.8 \pm 2.7 (20)	3.65	0.03

Remsen 1986), and this has been reported for several wader species (Cramp 1983). We pooled Ruff males of the same color type from their entire main breeding range and therefore much of the overlap in our sample might be due to size differences between sub-populations.

We argue further that the white plumage of small males may be a reliable signal (*sensu* Lyon and Montgomerie 1986) of their satellite status. If the white plumage reduces aggression from territorial males, such a signal would be favored. Thus, white males may indicate that they are less of a threat to the mating success of territorial males. Our hypothesis assumes that the copulation success of dark, independent males is higher than that of white satellites, which provides a possible test of the hypotheses. Existing data on this topic are contradictory. In one data set, independent males were about twice as successful as satellites, but in another the proportion of copulations was equal to the proportion of satellites and independent males (van Rhijn 1983).

Though we cannot reject the hypothesis that the polymorphism is maintained by equal genetic pay-offs, we suggest that the polymorphism of the Ruff may be determined by environmental rather than by purely genetic factors. More data on the relative copulation success of independent and satellite males are needed to understand the polymorphism in Ruffs.

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