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MIXED SEXUAL DIMORPHISM IN SEMIPALMATED PLOVERS¹

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Abstract. Sexually dimorphic species generally are characterized by having one sex consistently larger, and often brighter, than the other. Semipalmated Plovers (*Charadrius semipalmatus*) exhibit a pattern of mixed dimorphism with females that are heavier and having longer wings than males, whereas males have longer toes and bills, and are more colorful than females. Although we found weak evidence that male and female plovers mate assortatively with respect to body size, this likely resulted from birds of certain phenotypes breeding at different times. The mixed pattern of dimorphism in Semipalmated Plovers has probably resulted from different selection pressures, ecological and sexual, operating on different characters.

Key words: *Semipalmated Plover*, *Charadrius semipalmatus*, *sexual dimorphism*, *assortative mating*.

Hypotheses concerning the evolution and maintenance of sexual size dimorphism in birds generally focus upon benefits to one sex in terms of mating advantages (Darwin 1871) or benefits to both sexes in terms of reduced competition (Selander 1972). Most dimorphic taxa contain species that exhibit either “normal” size dimorphism, in which males are larger than females (e.g., Icterinae), or “reversed” size dimorphism, in which females are larger than males (e.g., Falconiformes). The suborder Charadrii (order Charadriiformes) is of particular interest in studies of sexual dimorphism because its species range from those in which males are much larger than females (e.g., Ruffs *Philomachus pugnax*, Prater et al. 1977) to those in which females are significantly larger than males (e.g., Jacanas *Jacana spinosa*, Jenni and Collier 1972). In rare cases, there is evidence for both normal and reversed size

dimorphism (mixed dimorphism) for different morphological characters within a species (e.g., Common Ringed Plover *Charadrius hiaticula*, Dement'ev et al. 1956, in Jehl and Murray 1986). Here we report on mixed dimorphism in the closely related Semipalmated Plover *Charadrius semipalmatus*.

Selection pressures responsible for the evolution and maintenance of sexually dimorphic characters may be ecological, for example if males and females are adapted to different feeding regimes, or sexual, if the possession of certain traits results in increased mating success for individuals of one sex. Assortative mating, defined as nonrandom mating with respect to some phenotypic character (Findley et al. 1988), may be indicative of active mate choice; if so, the expression of sexual dimorphism in such traits is likely maintained by sexual selection. Our second objective, therefore, is to test whether males and females mate assortatively with respect to any characters that differ between the sexes.

METHODS

We studied Semipalmated Plovers in the 1992–1996 breeding seasons in and around Churchill, Manitoba (58°45'N, 95°04'W). Adults were captured during the last two weeks of the 24-day incubation period, using walk-in traps, and were weighed to the nearest 0.1 g using a Pesola spring balance. Sexes were easily distinguished on the basis of auricular plumage (Cramp and Simmons 1983); ear coverts of females are the same brown as on the back, whereas those of males are solid black, contrasting with the brown back. Lengths of tarsus, culmen, and middle toe were measured with vernier calipers to the nearest 0.01 mm, whereas wing length was measured to the nearest 1 mm with a ruler. To document potential color differences between the sexes in addition to those used for sexing birds, we counted the number of brown feathers in the breast band and quantified (by length) the

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TABLE 1. Morphological measurements of male and female Semipalmated Plovers.

Character	male	n	female	n	m/f ^a	P
mass (g)	46.07 ± 0.20	150	47.76 ± 0.21	143	0.965	*
wing chord (mm)	123.70 ± 0.23	153	125.57 ± 0.23	145	0.985	*
tarsus (mm)	22.98 ± 0.10	153	22.82 ± 0.10	145	1.007	ns
middle toe (mm)	17.27 ± 0.11	122	16.84 ± 0.12	110	1.025	*
culmen (mm)	12.06 ± 0.04	150	11.85 ± 0.04	144	1.017	*
orange in culmen (mm)	5.37 ± 0.07	139	4.54 ± 0.07	129	1.183	*
number of brown feathers	3.04 ± 0.44	107	13.10 ± 0.46	99	0.232	*

* $P < 0.05$.^a Male to female ratio where 1 = monomorphism.

amount of orange in the culmen. In each year, one observer made all measurements, although during the study period three different observers were involved.

Preliminary analyses revealed significant between-year variation of first-time caught birds for tarsus and bill length, and amount of orange on the bill, whereas between-year differences in mass and wing chord approached significance. As it was unclear whether these differences reflected real variation between years or were due to measurement bias by the three researchers, we standardized measurements for each character by adding or subtracting a constant equal to the difference between the five-year mean for that character and the mean for that year. This eliminated between-year variation (whether real or artifactual) while maintaining within-year variation, and allowed us to pool data from the five breeding seasons.

Statistical differences for mass, wing chord, tarsus, and middle toe were determined using *t*-tests. Differences between males and females for the middle toe, the amount of orange in the culmen, and the number of brown feathers were analyzed with Mann-Whitney *U*-tests because these variables were not normally distributed. All tests were two-tailed as we did not predict *a priori* the direction of dimorphism. Pearson's and Spearman correlations were used for normally and nonnormally-distributed variables, respectively, to test for assortative mating. All probability values in Tables 1–3 were Bonferroni-adjusted.

RESULTS

Semipalmated Plovers exhibit a relatively low degree of sexual dimorphism, with substantial overlap be-

TABLE 2. Correlation coefficients between breeding pairs of Semipalmated Plovers for various morphological traits. All values are nonsignificant ($P > 0.05$) after Bonferroni corrections.

Character	<i>r</i> or <i>r_s</i>	n
mass	0.144	117
wing chord	-0.014	121
tarsus	-0.089	121
culmen	0.000	119
toe	0.132	92
orange in bill	-0.050	109
brown feathers	0.076	81

tween males and females for all characters measured. Those characters that differ significantly between males and females, however, indicate a mixed pattern of dimorphism (Table 1). If mass or wing chord is used as an indicator of overall body size, females are larger than males. Culmen and toe length, however, are significantly longer in males, and there is no difference between the sexes in tarsus length. In addition to auricular plumage differences used to identify the sexes, males have more orange in their bills and fewer brown feathers on their breast.

To determine whether Semipalmated Plovers mated assortatively on the basis of any of these characters, we first calculated pairwise correlations for each character for all mated pairs. We were particularly interested in possible correlations between characters indicating general body size (mass and wing chord) or bill length because some shorebirds are known to mate assortatively, either positively or negatively, with respect to these characters. Correlations of single characters indicate that male and female Semipalmated Plovers do not mate assortatively with respect to any of the measured traits (Table 2). However, there is weak evidence that heavy females are more likely to mate with males having longer wings ($r = 0.17$, $n = 119$, $P = 0.07$).

We then tested whether males or females having certain phenotypes were more likely to breed earlier as determined by clutch completion dates. Pairs within each season were separated into two groups, those nesting in the first half and last half of the nesting season; the two groups were then compared for differences in morphology for all years combined. In the case of renesting, only the first breeding attempt was used. The results indicate that those males that bred in the first half of the season had significantly longer wings than those that bred later. There were no other differences between the first and second half of the breeding season for any of the measured traits (Table 3).

DISCUSSION

Semipalmated Plovers exhibit mixed sexual dimorphism; males have longer bills than females and more contrasting plumage characteristics, whereas females are larger in overall body size. This mixed pattern of dimorphism, although unusual, has been observed in other shorebirds. If we assume that a male to female ratio of a particular character equaling 1.00 ± 0.01 or

TABLE 3. Measurements for birds breeding in the first (1) and second (2) half of the breeding season.

Character	male		female	
	1	2	1	2
mass (g)	46.50 ± 0.29	45.89 ± 0.35	48.45 ± 0.29	47.41 ± 0.34
wing (mm)	124.75 ± 0.27	122.67 ± 0.32*	125.95 ± 0.31	125.49 ± 0.37
tarsus (mm)	22.40 ± 0.12	22.77 ± 0.14	22.40 ± 0.10	22.57 ± 0.12
middle toe (mm)	17.40 ± 0.13	17.07 ± 0.16	16.86 ± 0.17	16.80 ± 0.20
culmen (mm)	12.16 ± 0.06	11.92 ± 0.08	11.85 ± 0.06	11.88 ± 0.07
orange (mm)	5.39 ± 0.09	5.29 ± 0.10	4.52 ± 0.12	4.61 ± 0.14
number of brown feathers	3.16 ± 0.45	2.53 ± 0.50	13.33 ± 0.77	12.84 ± 2.53

* $P < 0.05$.

less reflects monomorphism, then Common Ringed Plovers, Mongolian Plovers (*C. mongolius*), and Killdeers (*C. vociferus*) also apparently exhibit mixed dimorphism of different traits (although sample sizes are small for the first two species) (Jehl and Murray 1986). Closer examination of such species may be important in assessing various hypotheses concerning the selection pressures maintaining sexual dimorphism (Jehl and Murray 1986).

It is possible that current patterns of dimorphism in these species are simply products of historical selection and have no selective advantage in present populations. Evidence of similar patterns of dimorphism in closely related species with widely differing ecologies would support this hypothesis as it would suggest that such patterns were present in a common ancestor and did not arise independently due to different selection pressures operating on each species. Paton et al. (1994), for example, concluded that reversed dimorphism found in diurnal raptors is probably an ancestral condition although its magnitude in extant species depends on feeding habits. More complete information concerning phylogenetic relationships within the genus *Charadrius* (containing 31 species; Sibley and Monroe 1990) are required to test this hypothesis. However, such an explanation is unlikely given that morphological traits, particularly those directly related to body size and feeding, are probably under relatively strong selection pressure (Price and Boag 1987).

It is more likely that the presence of mixed dimorphism is the result of sexual and ecological selection working simultaneously on different characters. Jönsson (1987), for example, found that male Dunlins (*Calidris alpina*) are lighter and have shorter wings and bills, relative to their body size, than females. He proposed that small size in males might be advantageous in minimizing energy expenditure during aerial displays and/or while brooding young, whereas large size in females would enable them to compete more effectively for mates or produce larger eggs and/or clutches. These explanations also may apply to Semipalmated Plovers in which males sometimes perform flight displays in excess of 4 min in contests with other territorial males (M. S. Blanken, pers. comm.). Sexual dimorphism in bill size most often reflects differences in feeding behavior, and likely functions to reduce direct competition between males and females (Selander 1972). While the difference in absolute bill size for Semipalmated Plovers is small (12.06 vs. 11.85 mm

for males and females, respectively), the relative difference is larger, considering that overall female body size is greater than that of males. This relationship, and the observation that males have slightly longer toes than females, suggests the possibility of differences in foraging habitat or behavior.

Evidence of assortative mating for a particular trait or set of traits often is used to implicate sexual selection as the underlying force driving the development of sexual dimorphism of that trait. Some shorebirds are known to mate assortatively, either positively or negatively, with respect to certain characters. These include Stilt Sandpipers (*Micropalama himantopus*) and Least Sandpipers (*Calidris minutilla*) in which small males mate with large females (Jehl 1970), Dunlins, in which small, short-billed males pair with large, long-billed females (Jönsson 1987), and Little Ringed Plovers (*Charadrius dubius*) in which large males mate with large females (Hedenström 1987). In this study, we found weak evidence that Semipalmated Plovers mate assortatively by size, with heavier females pairing more often with larger (as measured by wing length) males. However, this should not be taken as evidence of selective mate choice; such pairings also may result from ecological constraints (Cooke and Davies 1983). For example, differential spring arrival times of large and small birds may result in individuals of a certain size-group being more available in the pool of potential mates. In our study area, males breeding during the first half of the season do have significantly longer wings, and females are slightly heavier, although not significantly so. Alternatively, if the size of certain physical characters is age-related, positive assortative mating is expected if males and females from similar age-cohorts are more likely to pair. In both these situations, assortative mating may be based on nongenetic size differences between individuals, and thus sexual selection may not be a factor in the maintenance of sexual dimorphism.

Although it is not clear which characters have diverged because of sexual or ecological factors, the same evolutionary force is unlikely to have produced the mixed pattern of sexual dimorphism found in Semipalmated Plovers. Further studies concerning the phylogenetic relationship of closely related species, potential differences in the feeding behavior of males and females, and the reproductive success of individuals having different phenotypes are required to deter-

mine selection pressures responsible for sexual dimorphism in this and other species.

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CORTICOSTERONE LEVELS DURING NEST DEPARTURE OF JUVENILE AMERICAN KESTRELS¹

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Abstract. Many avian behavior patterns, such as breeding, migration and territoriality, are correlated with changes in hormone levels. Elevated levels of corticosterone, an adrenal steroid hormone, are associated with increased foraging and increased activity levels in birds. Young birds about to take their first flight may benefit from elevated plasma corticosterone levels that facilitate locomotor activity and foraging

behavior while they are developing flight and hunting skills. I examined the relationship between corticosterone levels and the timing of nest departure in nestling American Kestrels (*Falco sparverius*). American Kestrels are cavity nesters and typically depart from the nest between 25–30 days of age, when they take their first flight. I collected blood from 21–25-day-old kestrels and monitored nest boxes to determine date of nest departure. Consistent with my prediction, as birds prepared to depart from the nest their plasma corticosterone levels increased significantly. The relationship between corticosterone levels and nest departure may

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