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Assortative Mating and Sexual Size Dimorphism in Western and Semipalmated Sandpipers

BRETT K. SANDERCOCK¹

Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

Sexual dimorphism in body size is widespread among animals, and most explanations for the evolution of dimorphism can be grouped into two categories: (1) sexual selection, and (2) intraspecific niche differentiation (Jehl and Murray 1986, Shine 1989). Sexual selection clearly has been important in shorebirds (suborder Charadrii), because the direction and magnitude of size dimorphism are related to both mating system and the duration of parental care (Jönsson and Alerstam 1990, Reynolds and Székely 1997). Typically, the sex that competes for mating opportunities is larger, and this is true for most polygynous shorebirds (males larger) and species with sex-role reversal where females are larger (Jehl and Murray 1986, Jönsson and Alerstam 1990). It is more difficult to explain, however, why females are the larger sex in many shorebirds that mate mo-

nogamously (Jehl and Murray 1986, Olsen and Cockburn 1993).

Female-biased sexual size dimorphism could evolve if the sexes become adapted to different ecological conditions (Shine 1989). Alternatively, female-biased dimorphism may result if sexual selection acts such that fitness covaries positively with body size for females but negatively for males. Energy storage capacity increases with structural size, and large-bodied female sandpipers may have an advantage if they are able carry resources that allow them to breed earlier or lay larger eggs (Erckmann 1981, Jehl and Murray 1986, Jönsson 1987). On the other hand, energy efficiency decreases with increasing body size (Jönsson and Alerstam 1990). Male calidrine sandpipers often give complex display flights during courtship (Miller 1979), and small body size may allow for increased agility in these aerial displays (Jehl and Murray 1986, Blomqvist et al. 1997). Negative assortative mating could further increase selection on body size if birds pair with respect to morphology. Examples of negative assortative mating are rare in birds, and they usually are based on color-morph preferences (Partridge 1983, Houtman

¹ Present address: University of California, Ecosystem Sciences Division, Department of Environmental Science, Policy and Management, 151 Hilgard Hall, Berkeley, California 94720, USA. E-mail: bsanderc@nature.berkeley.edu

and Falls 1994). Nevertheless, negative assortative mating with respect to body size has been reported in at least three species of monogamous sandpipers: Least Sandpipers (*Calidris minutilla*; Jehl 1970), Stilt Sandpipers (*C. himantopus*; Jehl 1970), and Dunlins (*C. alpina*; Jönsson 1987).

Western Sandpipers (*Calidris mauri*) have the highest female-biased size dimorphism among all of the monogamous sandpipers (Jehl and Murray 1986:50). If sexual selection maintains sexual size dimorphism in monogamous shorebirds, the processes might be most pronounced in this species. To evaluate the potential importance of sexual selection, I examined whether there was: (1) assortative mating for body size, and/or (2) a relationship between fecundity and body size in Western Sandpipers and Semipalmated Sandpipers (*C. pusilla*).

Methods.—I studied Western and Semipalmated sandpipers at a 4-km² study site located 21 km east of Nome, Alaska (64°20'N, 164°56'W) during May to July, 1993 to 1995. Like most monogamous shorebirds, males are territorial and give display flights during courtship. Females lay a modal clutch size of four eggs, both sexes incubate the clutch, and males provide most of the parental care after hatching (Gratto-Trevor 1991, Sandercock 1997). Nests were located by observing sandpipers that flushed or gave distraction behaviors. Egg-laying rates were 0.8 eggs/day, and duration of incubation was 20 (Semipalmated Sandpiper) or 21 days (Western Sandpiper; Sandercock 1998). Date of clutch initiation was calculated by backdating from egg laying, stage of incubation (determined by floating eggs in water), or date of hatching. Clutch size was determined by revisiting nests found during laying until egg number was unchanged. Egg length (*L*) and breadth (*B*) were recorded with calipers, and egg volume (*V*) was estimated using:

$$V = 0.47LB^2 \quad (1)$$

(B. Sandercock unpubl. data).

Incubating birds were captured in walk-in traps placed over the clutch, and both parents were captured on most nests. Each bird was individually marked with colored leg bands, and I measured exposed culmen length, tarsus length, and length of flattened wing. Plumage is sexually monochromatic in both species. Western Sandpipers were sexed by culmen length (<24.2 mm = male, >24.8 mm = female) because previous work with sacrificed birds has shown that this technique is 95% reliable (Page and Fearis 1971, Cartar 1984). A small proportion of Western Sandpipers (3.6%, *n* = 196) had a culmen of intermediate length (24.2 to 24.8 mm); I inferred the sex of these birds from the culmen measurements of their mates. Semipalmated Sandpipers were more difficult to sex by external morphology alone. A subsample of birds (*n* = 15) was sexed as males by their behavior (i.e. courtship displays, copulatory posi-

tion); these males had smaller culmens than their mates in almost all of their pairings (96.2%, *n* = 26). Moreover, individuals that paired with different birds in separate years usually had mates with culmens that consistently were either longer or shorter than their own (88%, *n* = 32 possible cases). Therefore, I assumed that the bird with the longest culmen in each pair was the female. Errors in sexing should have had little effect on my conclusions because the few exceptions (3 of 4) usually were due to pairs of Semipalmated Sandpipers that had culmens of similar length (i.e. <0.8 mm difference).

Statistics were calculated using SAS (SAS Institute 1990); all tests were two-tailed and considered significant at probability levels less than 0.05. Parametric tests were used because all of the variables were normally distributed (Shapiro-Wilk's test, *P* > 0.05), with the exception of timing of laying. Timing of laying varied among years, but egg volume and modal clutch size did not (Sandercock 1997). I standardized clutch initiation dates by subtracting the median laying date (for each species in a given year) and then rank-transforming the adjusted date. I calculated a mean egg volume for each clutch, and pooled clutches of two and three eggs in the analysis of clutch size. Some birds and pairs were observed in more than one year, but I included reproductive data only from the first year that a bird was captured. In the analysis of assortative mating, each unique pair was included only once to avoid pseudoreplication.

Univariate measures often are used to describe avian morphology, but such variables may not be representative of overall body size (Freeman and Jackson 1990). I used principal component analysis to create an index of body size based on culmen, tarsus, and wing lengths (Rising and Somers 1989). I used the morphometrics from the first capture occasion and treated each species separately. All of the eigenvectors of principal component 1 (PC1) showed positive loadings, and PC1 explained 70.4% and 68.5% of the variation in body size of Western and Semipalmated sandpipers, respectively.

Results.—Female sandpipers were significantly larger than males in all univariate measures of body size (Table 1). The sexual size dimorphism of Western Sandpipers (culmen 16.3%, tarsus 6.2%, wing 3.6%) was greater than that of Semipalmated Sandpipers (culmen 9.0%, tarsus 3.4%, wing 2.0%). Univariate measures of body size were not significantly correlated within mated pairs of Western Sandpipers (culmen, *r* = 0.14, *P* = 0.10; tarsus, *r* = 0.10, *P* = 0.27; wing, *r* = 0.17, *P* = 0.07, *n* = 126) or Semipalmated Sandpipers (culmen, *r* = -0.05, *P* = 0.60; tarsus, *r* = -0.14, *P* = 0.11; wing, *r* = -0.08, *P* = 0.40, *n* = 118). Multivariate techniques gave the same results: female body size and male body size (PC1) were not correlated in either sandpiper species (Western Sandpiper, *r* = 0.13, *P* = 0.16; Semipalmated Sandpiper, *r* = -0.14, *P* = 0.13). The power to detect a

TABLE 1. Univariate measurements ($\bar{x} \pm SD$) of Western Sandpipers and Semipalmated Sandpipers captured near Nome, Alaska.

Variable	Females	Males	<i>t</i>	<i>P</i>
Western Sandpipers				
Culmen length (mm)	26.4 ± 1.1	22.4 ± 1.0	27.3	<0.001
Tarsus length (mm)	23.7 ± 0.8	22.2 ± 0.8	12.9	<0.001
Wing length (mm)	101.1 ± 2.6	97.5 ± 2.5	9.7	<0.001
<i>n</i>	98	98	—	—
Semipalmated Sandpipers				
Culmen length (mm)	18.7 ± 0.9	17.1 ± 0.8	13.1	<0.001
Tarsus length (mm)	22.4 ± 0.8	21.6 ± 0.8	7.5	<0.001
Wing length (mm)	99.1 ± 2.7	97.0 ± 2.5	5.5	<0.001
<i>n</i>	106	95	—	—

correlation was high, because an *r*-value higher than 0.18 would have been significant in either species.

There was a significant relationship between body size and date of clutch initiation in male Semipalmated Sandpipers ($y = 72.3 - 9.74x$; $r^2 = 0.04$, $t = -1.19$, $P = 0.049$) and between body size and date of clutch initiation in female Western Sandpipers ($y = 52.8 + 10.3x$; $r^2 = 0.05$, $t = 2.17$, $P = 0.03$). Large males and small females nested significantly earlier, trends contrary to the prediction that early nesting acts as a disruptive selective pressure on body size. Less than 7% of the variation in date of clutch initiation was explained by body size in either species. Body size did not differ between females that laid two or three versus four eggs (*t*-tests, $P > 0.40$). Thus, large and small females did not differ in clutch size. Finally, there was a significant relationship between mean egg volume and female body size in both Western Sandpipers ($y = 6.86 + 0.22x$; $r^2 = 0.15$, $t = 3.96$, $P < 0.0005$) and Semipalmated Sandpipers ($y = 6.23 + 0.11x$; $r^2 = 0.09$, $t = 3.21$, $P < 0.005$). Female body size accounted for 9 to 15% of the variation in egg volume in both species. Mean egg volume increased by 17% and 9% over the range of female body sizes in Western and Semipalmated sandpipers, respectively.

Discussion.—Western and Semipalmated Sandpipers were sexually dimorphic in body size, and the greatest degree of dimorphism was in culmen length. This is consistent with previous reports for these and other shorebird species (Ouellet et al. 1973, Cartar 1984, Mueller 1989). Despite the pronounced difference in culmen length between female and male Western Sandpipers (16.3%; range 2 to 16% for other monogamous sandpipers; Jehl and Murray 1986, Jönsson and Alerstam 1990), I found no evidence for assortative mating in this species or in Semipalmated Sandpipers.

Assortative mating for body size can be produced by passive size-dependent variation in the availability of mates, or by active mate choice (Cooke and Davies 1983). Positive assortative mating for body size has been reported in Ringed Plovers (*Charadrius du-*

bius; Hedenström 1987) and Semipalmated Plovers (*C. semipalmatus*; Teather and Nol 1997), but older, larger birds may have paired together. Negative assortative mating for body size has been reported in Dunlins, Least Sandpipers, and Stilt Sandpipers (Jehl 1970, Jönsson 1987). Differences in reproductive biology cannot explain why Western Sandpipers and Semipalmated Sandpipers did not show assortative mating. All five calidrine species are small, male-territorial shorebirds that breed monogamously in the arctic. My conclusions should be robust because sample sizes (118 to 126 pairs) were greater than those of Jehl (29 to 41 pairs) and Jönsson (33 pairs). I note, however, that differences in methodology may have been important. Jehl (1970) and Jönsson (1987) calculated multiple correlations between univariate measures of body size and fecundity. Their results might have been nonsignificant if they had adjusted the degrees of freedom for the number of tests (Rice 1989) or described body size with multivariate statistics (Rising and Somers 1989, Freeman and Jackson 1990). Moreover, neither Jehl nor Jönsson compared the morphology of mated pairs directly. Both authors regressed an index of intrapair dimorphism (a difference or ratio between female and male body size) on timing of breeding (date of hatching or egg-laying), and found that early breeding pairs had greater dimorphism. However, a relationship between timing of breeding and body size in one sex could produce the same result without negative assortative mating. Therefore, the evidence for negative assortative mating in calidrine sandpipers seems weak.

The relationship between timing of breeding and body size was significant in this and in other studies of sandpipers (Jehl 1970, Erckmann 1981:228, Jönsson 1987). Unlike previous studies, however, I found no evidence that small males or large females bred earlier. My results do not support the idea that size-dependent variation in timing of laying has led to sexual size dimorphism. Moreover, it is unclear whether early nesting confers a reproductive advantage in sandpipers. Predation on shorebird nests can

be high early in the breeding season (Byrkjedal 1980, Pienkowski 1984). Low natal philopatry makes it difficult to measure survival rates of juvenile shorebirds (Thompson et al. 1994), but Lank et al. (1985) found no evidence of seasonal declines in the recruitment of Spotted Sandpipers (*Actitis macularia*).

In my study, large females laid large eggs, as found for several other species of shorebirds (Miller 1979, Jönsson 1987, Blomqvist and Johansson 1995). Egg size has a residual positive effect (controlling for parent quality) on the growth and survival of young in other precocial birds (e.g. Dawson and Clark 1996), and large body size may confer a fitness advantage to female sandpipers. The relationship between egg size and body size could be confounded by female age (Cooch et al. 1992), but yearling breeders were relatively uncommon at Nome, and egg size did not increase with relative age (Sandercock 1997). The most parsimonious explanation for the lack of a relationship between body size and egg number is the low variability in clutch size; most females (66.7 to 91.7%) laid four eggs (Sandercock 1997).

Intrasexual competition for mates could lead to sexual size dimorphism through variation in mating success. Erckmann (1981) and Jehl and Murray (1986) argued that males are the smaller sex because they give display flights during courtship, and aerial agility is predicted to increase with small body size (Andersson and Norberg 1981). Recent studies support this hypothesis: the rate and duration of aerial display is negatively correlated with body size in male Dunlins (Blomqvist et al. 1997), and male Northern Lapwings (*Vanellus vanellus*) that give complex aerial displays obtain more mates (Grønseth 1996). Male body size was not related to timing of laying in this study, but I examined only sandpipers that were paired. Not all males obtain a mate (Gratto-Trevor 1991), and these could be large-bodied individuals.

Jehl and Murray (1986:50–51) argued that sexual selection alone explains sexual dimorphism in Western Sandpipers. However, I found little evidence that sexual-selection processes are important in this species or in Semipalmated Sandpipers. Moreover, the aerial-agility hypothesis does not explain why sexual dimorphism is highest in culmen length (i.e. a trophic structure; Mueller 1989). Dimorphism in bill length leads to sex-specific foraging rates in woodpeckers (Selander 1966), hummingbirds (Temeles and Roberts 1993), and Bar-tailed Godwits (*Limosa lapponica*; Pierre 1994). It seems feasible that sexual dimorphism in sandpipers also could be an adaptation for niche specialization. During migration, long-billed Semipalmated Sandpipers forage in softer sediments than do short-billed birds (Harrington 1982), and females take larger prey items (Gratto et al. 1984). A long bill may aid females in accessing additional re-

sources for egg laying, particularly in species like Western Sandpipers and Semipalmated Sandpipers, where the short-billed males precede the females north during spring migration (Harrington 1982, Butler et al. 1987). Male sandpipers often are the sole providers of parental care after the young hatch (Gratto-Trevor 1991), and a short bill could help males to glean prey in terrestrial habitats (Jönsson 1987). Future research should examine whether sexual dimorphism in bill morphology affects foraging rates and/or microhabitat preferences of female and male sandpipers.

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Subadult Movement Patterns of the Endangered Hawaiian Stilt (*Himantopus mexicanus knudseni*)

J. MICHAEL REED,^{1,6} MICHAEL D. SILBERNAGLE,² KAREN EVANS,³

ANDREW ENGLISH, JR.,⁴ AND LEWIS W. ORING⁵

¹Department of Biology, Tufts University, Medford, Massachusetts 02155, USA;

²U.S. Fish and Wildlife Service, 66-590 Kamehameha Highway, Room 26, Haleiwa, Hawaii 96712, USA;

³U.S. Fish and Wildlife Service, P.O. 50167, Honolulu, Hawaii 96850, USA;

⁴Ducks Unlimited, 3074 Gold Canal Drive, Rancho Cordova, California 95670, USA; and

⁵Program in Ecology, Evolution, and Conservation Biology, University of Nevada, 1000 Valley Road, Reno, Nevada 89512, USA

Data on individual movement patterns are important for understanding foraging patterns, mate acquisition, and dispersal (Baker 1978, Krebs and Inman 1992, Colwell and Oring 1989, Reed et al. 1999). More recently, requirements for conservation biology have resulted in increased interest in the movements of individual (abilities and patterns) because of their relationships to population persistence in fragmented landscapes. Immigration is necessary to maintain local components of metapopulations (Brown and Kodric-Brown 1977), and the parameter that determines the amount of interaction among components of a metapopulation is dispersal (Hansson 1991, Wu et al. 1993).

In this paper, we present data on movements of subadult Hawaiian Stilts (*Himantopus mexicanus knudseni*), an endangered subspecies confined to the main Hawaiian Islands. Most of the data are from the island of Oahu, but we also present information on movements among islands across the range of the subspecies. Hawaiian Stilts forage in shallow water and nest on adjacent flats and embankments (Coleman 1981). Current wetland area in Hawaii is less than 30% of its original extent (Dahl 1990, English and Pratt 1993), and the population size of stilts de-

pends partly on agricultural and aquacultural practices (e.g. runoff from taro, rice, and sugarcane farming) that provide breeding and foraging habitat (Broshers 1979, Griffin et al. 1989). Dependence on agriculture, coupled with habitat conversion for housing and business, has resulted in a fragmented and reduced wetland landscape (Shallenberger 1977, Coleman 1981, Griffin et al. 1989) and disjunct distributions of waterbirds (Reed and Oring 1993, English and Reid 1994, Reed et al. 1994). Hawaiian Stilt population size decreased substantially early in this century until the 1940s (Munro 1944) but increased during the last 50 years (Reed and Oring 1993) to its current population size of around 1,300. Hawaiian Stilts appear to be habitat limited (Reed et al. 1998) and are threatened constantly by exotic predators and exotic wetland plants that make wetlands unsuitable for breeding and foraging (English and Reid 1994). This shorebird study is unusual in that it focuses on short-term, predispersal movements. Although data on shorebird movements exist for some species, they typically focus on dispersal, migration, or foraging (e.g. Oring and Lank 1984, Warnock et al. 1995, Butler et al. 1997).

Study system.—Hawaiian Stilts inhabit seven islands (Hawaii, Kauai, Maui, Molokai, Oahu, Niihau, Lanai), although only the Oahu, Maui, and Kauai

⁶ E-mail: mreed@tufts.edu