

by hierarchy may be regarded as the greatest threat, in terms of either jumping the queue or courting females. A second explanation for the pattern of stronger response to own-colony song is that foreign males in general are so strongly discriminated against in mate choice by local females that they represent little threat to an established male's mating success. A third explanation is that males use the songs they hear locally to learn what the species song ought to sound like, and respond less to foreign songs to the extent that they differ from this standard; lower response to foreign song under this hypothesis is simply a non-adaptive consequence of song learning. Further research would be needed to test these alternatives.

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SPERM COMPETITION AND SPERM LENGTH IN SHOREBIRDS¹

DOMINIC D. P. JOHNSON AND JAMES V. BRISKIE²

Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, United Kingdom, e-mail: dominic.johnson@zoo.ox.ac.uk

Abstract. We investigated how sperm morphology varies across 16 species of shorebirds in the Scolopacidae, Charadriidae, and Jacanidae. Sperm were significantly longer in nonmonogamous than in socially monogamous species. Nonmonogamous species also

had significantly longer midpieces and tails than monogamous species. As the midpiece houses the mitochondria for powering the tail, this suggests that sperm competition may select for greater investment in mobility. After controlling for phylogeny and male body mass, sperm tail length was correlated positively to relative testis size. There was no evidence that variation in sperm morphology was related to either male body mass (through allometry) or egg size (via linkage disequilibrium). Instead, our results suggest that sperm size in shorebirds increases with the intensity of sperm competition.

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²Current address: Department of Zoology, Private Bag 4800, University of Canterbury, Christchurch, New Zealand.

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Sperm length ranges from 43 μm in the Red-backed Shrike (*Lanius collurio*) to 292 μm in the Reed Bunting (*Emberiza schoeniclus*), or almost a 7-fold difference among species of birds (Briskie et al. 1997). Although a number of hypotheses have been proposed, the functional significance of this variation remains unclear (Briskie and Montgomerie 1992, 1993, Briskie et al. 1997).

At the simplest level, interspecific diversity in sperm morphology could be a product of allometry. Many organs covary with body size, and some species may have larger sperm as a consequence of their larger body size. For example, large species of butterflies tend to have longer sperm than small species (Gage 1994). Alternatively, sperm size may be determined through a process of linkage disequilibrium (Halliday and Arnold 1987). Male and female gametes share similar embryological origins, so it is possible that selection on egg size (perhaps for greater precociality) may inadvertently change sperm size. Under this hypothesis, sperm size is predicted to increase or decrease in concert with changes in egg size across species. A third possible explanation for interspecific diversity in sperm morphology is the action of sperm competition (Parker 1970). If fertilization success depends upon the number of sperm inseminated by each male, selection should favor males that produce large quantities of sperm to dilute rival ejaculates (Martin et al. 1974). Producing sperm can be costly (Dewsbury 1982, Olsson et al. 1997), and thus males are expected to increase sperm numbers by reducing sperm size (Parker 1982). However, this prediction has not been supported by recent studies that have found sperm are longer in species experiencing intense sperm competition (Gomendio and Roldan 1991, Gage 1994, Briskie et al. 1997).

In this study we examine sperm morphology in shorebirds to determine whether variation in this group can best be attributed to allometry, differences in relative egg size, or sperm competition intensity. Shorebirds provide an ideal group to examine these three hypotheses because, while being closely related, they also exhibit a diverse range of mating systems, egg sizes, and body sizes.

METHODS

Sperm morphology was compared among 16 species of shorebirds from the families Scolopacidae (13 species), Charadriidae (2 species), and Jacanidae (1 species; Table 1). All sperm originated from birds collected from Churchill, Manitoba, Canada except for the Wattled Jacana (Panama), American Woodcock (Georgia, USA), Red Phalarope (Igloolik, Nunavut Territory, Canada), Pectoral Sandpiper (Taymyr Peninsula, Russia) and Ruff (captive flock, Simon Fraser University, Canada; scientific names in Table 1). The reproductive organs, including the testes and vas deferens, were removed within 3 hr of death and preserved in 10% buffered formalin until dissected. The number of samples per species ranged from 1 to 3 (mean 1.8 birds species⁻¹) for a total of 29 individuals.

Although the number of individuals collected per species was small, previous studies have shown that most variation in sperm size is due to differences among species rather than within a species (Briskie and Montgomerie 1992). Thus, even a sample from a single individual can provide a fairly accurate measure of sperm morphology for that species.

Sperm samples were obtained from the distal end of the vas deferens as sperm collected from the testis have not completed development. An incision was made in the vas deferens near the cloaca. Sperm and seminal fluid were then extracted with a micropipette and mounted onto a slide and allowed to air dry. For most individuals, we were able to measure 20–30 sperm, but a few samples were damaged or few sperm were present in the vas deferens and so we could only measure 5–10 sperm. All sperm were measured with an ocular micrometer at 700 \times magnification under a light microscope. Four measurements were made of each sperm: (1) combined head and acrosome length, (2) midpiece length, (3) tail length, and (4) total length (sum of measures 1 to 3). We could not reliably differentiate the boundaries of the head and midpiece in the Jacana, White-rumped Sandpiper, and the two species of Charadriidae using bright-field microscopy. Our analysis of variation in these sperm components was therefore limited to 12 species in the Scolopacidae. As this subset includes species with both monogamous and nonmonogamous mating systems, it seems unlikely these exclusions bias the results in any particular direction.

To compare how sperm morphology varies among species, a number of life history variables were collected from the literature. Male and female body mass was obtained from Dunning (1993). Measurements of egg length and breadth were taken from Harrison (1975, 1978) and an egg volume index calculated as: volume index = length \times width². The social mating systems of waders were obtained from del Hoyo et al. (1996) and Cramp and Simmons (1983). We divided species into those with social mating systems that could be classified as monogamous and those species that formed "nonmonogamous" social bonds. Non-monogamous mating systems included polyandrous, polygynous, and lek breeding species. We assumed that species in this category experience higher levels of sperm competition than socially monogamous species (Birkhead and Møller 1992). Recent estimates of multiple paternity using DNA profiling of Red Phalaropes (6.5%; Dale et al. 1999), Wattled Jacana (17.9%; Emlen et al. 1998), Buff-breasted Sandpiper (*Tryngites subruficollis*, 40%; Lanctot et al. 1997), and Ruff (59%; Lank et al. 1995, D. B. Lank, pers. comm.) support this assumption. In contrast, extra-pair paternity rates in socially monogamous species of shorebirds are relatively low: Pierce and Lifjeld (1998) report an extra-pair paternity rate of 1.2% in the Purple Sandpiper (*Calidris maritima*), and Heg et al. (1993) found that only 1.5% of chicks were the result of extra-pair matings in the Eurasian Oystercatcher (*Haematopus ostralegus*). Nevertheless, paternity patterns are not known for most of the species in our sample, and so we also used relative testis size as a measure of sperm competition intensity (Møller and Briskie 1995). Testis

size was measured directly from each specimen from which sperm were collected. Testis length was used as an index of testis size and was measured to the nearest 0.5 mm with calipers. Only testis samples in which sperm were being produced were used in this analysis. The complete data set is given in Table 1.

Because all species studied are close relatives (all three families are members of the suborder Charadrii), differences among species are likely the result of differing selective pressures rather than different phylogenetic histories. However, as phylogenetic effects cannot be ruled out, the methods described by Harvey and Pagel (1991) were used to control for phylogenetic inertia. A recent phylogeny of the Charadriiformes by Szekely and Reynolds (1995) was used to construct a cladogram for the species in our study (Fig. 1). As the Ruff was not included in this cladogram, we placed it as a sister species to the *Calidris* sandpipers, a position suggested by other authors (Pitelka et al. 1974, van Rhijn 1991). The data were analyzed using the Comparative Analysis by Independent Contrasts Method (CAIC) by Purvis and Rambaut (1994). This method identifies contrasts for each node in the phylogeny that exhibits variation in the test variable. Sample sizes in statistical analyses are therefore the number of independent contrasts and not the number of species originally used in the analysis. Because of small sample sizes, contrasts for some comparisons have low statistical power. For example, mating system changed only six times in our sample of species. Therefore, we also used the raw data in these analyses and examined the contrasts as far as possible. Independent contrasts for continuous variables were tested by simple or multiple regression, forced through the origin (Harvey and Pagel 1991). A one-sample *t*-test was used for comparing contrasts between monogamous and nonmonogamous species (under the null hypothesis of a mean of zero). For ease of interpretation, we present our results using both the raw data as independent points, and as contrasts.

Values present are means \pm SE.

RESULTS

Total sperm length ranged from to 57.0 μ m in the Semipalmated Plover to 133.2 μ m in the Ruff (Table 1). In general appearance, sperm from all three families were similar; however, sperm from the family Scolopacidae had a conspicuous spiral or wavy shape. The number of waves along the head and midpiece was typically three in all species except the Red Phalarope, in which only two waves were present. Neither the plovers (Charadriidae) nor the Wattled Jacana (Jacanidae) had a readily defined midpiece and waves were only weakly developed.

Each of the three sperm components varied from species to species. The tail was the single largest component of the sperm, varying from 53.1% of total length in the American Woodcock to 78.6% of total length in the Lesser Golden Plover ($68.9 \pm 1.8\%$). Midpiece length ranged from 8.6% of total sperm length in the Whimbrel to 23.2% in the American Woodcock ($13.3 \pm 1.1\%$), while the relative length of the head (including acrosome) varied from 15.3% in the Red Phalarope to 24.6% in the Ruff ($19.8 \pm 0.8\%$).

Tail length was correlated positively with both midpiece ($r = 0.73$, $F_{1,11} = 11.3$, $P < 0.01$) and head length ($r = 0.73$, $F_{1,11} = 11.3$, $P < 0.01$). Midpiece length also was correlated positively with head length ($r = 0.92$, $F_{1,11} = 51.8$, $P < 0.001$). Increase in the total length of sperm was thus the result of concomitant increases in the size of each component.

There was no support for the hypothesis that increased sperm size is an allometric response to increased male body size. No significant relationship was found between male body mass and any measure of sperm size. Neither tail length ($r = 0.23$, $F_{1,10} = 0.6$, $P = 0.47$), midpiece length ($r = 0.20$, $F_{1,10} = 0.4$, $P = 0.54$), head length ($r = 0.37$, $F_{1,10} = 1.6$, $P = 0.24$), nor total length ($r = 0.28$, $F_{1,14} = 1.2$, $P = 0.30$) were significantly related to male body mass when controlled for phylogeny.

The linkage disequilibrium hypothesis predicts that sperm are larger in species with larger eggs. In a multiple regression analysis (controlling for female body mass and phylogeny), total sperm length (partial $F_{1,13} = 1.2$, $P = 0.29$) was not significantly correlated with egg size. There also were no significant correlations between egg size and sperm tail length (partial $F_{1,9} = 0.01$, $P = 0.95$), midpiece length (partial $F_{1,9} = 1.0$, $P = 0.34$), or head length (partial $F_{1,9} = 0.6$, $P = 0.46$). This suggests that larger sperm did not evolve as a consequence of increases in egg size.

Total sperm length, as well as the length of each of the three component parts, was greater in nonmonogamous than in socially monogamous species (Table 2). All comparisons were significant if species are treated as independent data points. Phylogenetic contrast analysis was limited by the small number of contrasts between monogamy and nonmonogamy. However, in all cases the contrasts were positive for both mating system and sperm length. This indicates that an evolutionary change in mating system from monogamy to nonmonogamy was significantly associated with an increase in total sperm length (one sample *t*-test: $t_2 = 3.84$, $P = 0.01$) as well as in the length of the tail ($t_4 = 2.96$, $P = 0.04$) and midpiece ($t_3 = 4.53$, $P = 0.02$). The combined head and acrosome length ($t_3 = 2.48$, $P = 0.09$) did not differ significantly between monogamous and nonmonogamous species although all contrasts were positive for both variables.

An increase in sperm size also was observed when testis length was used as an index of sperm competition intensity. Total sperm length increased with relative testis length although this difference was not quite significant (two-tailed test: partial $F_{1,13} = 4.2$, $P = 0.06$). This pattern is driven by the significant relationship between tail length and relative testis length (Fig. 2; partial $F_{1,9} = 5.6$, $P = 0.02$) as neither midpiece length (partial $F_{1,9} = 0.3$, $P = 0.29$) nor head length (partial $F_{1,9} = 0.1$, $P = 0.39$) was correlated with testis size.

DISCUSSION

Sperm length was highly variable among the species of shorebirds we examined. Although there are nonadaptive reasons that might explain this variation, we were able to reject the hypotheses that variation in sperm length is due to either allometry with body size

TABLE 1. Social mating system, mean sperm length, male and female body mass, testis length, and egg size for birds used in this study. All body masses taken from Dunning (1993); egg size indices were calculated from measurements provided by Harrison (1975, 1978).

Family/species	Mating system	Sperm length (μm)				Male (female) mass (g)	Testis length (mm)	Egg size index
		Total	Tail	Midpiece	Head			
Charadriidae								
Semipalmated Plover (<i>Charadrius semipalmatus</i>)	Monogamy	57.0	44.4	—	—	47.4 (46.1)	7.0	17.5
Lesser Golden Plover (<i>Pluvialis dominica</i>)	Monogamy	67.2	52.8	—	—	145.0 (145.0)	12.0	52.2
Jacaniidae								
Wattled Jacana (<i>Jacana jacana</i>)	Polyandry	91.0	68.9	—	—	78.9 (112.0)	17.0	14.5
Scolopacidae								
American Woodcock (<i>Scolopax minor</i>)	Polygyny	99.7	52.9	23.1	23.7	176.0 (219.0)	9.1	32.0
Common Snipe (<i>Gallinago gallinago</i>)	Polygyny	68.5	46.6	9.5	12.3	128.0 (116.0)	15.5	30.5
Whimbrel (<i>Numenius phaeopus</i>)	Monogamy	61.7	45.9	5.3	10.4	355.0 (404.0)	16.7	102.3
Short-billed Dowitcher (<i>Limnodromus griseus</i>)	Monogamy	62.8	45.2	6.0	11.6	111.0 (116.0)	9.0	34.5
Red Phalarope (<i>Phalaropus fulicaria</i>)	Polyandry	97.7	70.3	12.5	14.9	50.2 (61.1)	11.5	14.5
Lesser Yellowlegs (<i>Tringa flavipes</i>)	Monogamy	66.4	45.5	7.4	13.6	81.0 (81.0)	9.1	35.3
Stilt Sandpiper (<i>Micropalama himantopus</i>)	Monogamy	60.7	39.1	7.5	14.1	55.8 (60.4)	6.5	13.2
Ruff (<i>Philomachus pugnax</i>)	Lek	133.2	78.3	22.2	32.8	163.0 (95.0)	20.5	41.4
Semipalmated Sandpiper (<i>Calidris pusilla</i>)	Monogamy	62.5	43.3	8.2	10.9	28.1 (28.1)	9.2	22.5
White-rumped Sandpiper (<i>C. fuscicollis</i>)	Polygyny	68.8	—	—	—	44.9 (44.9)	10.3	19.6
Least Sandpiper (<i>C. minutilla</i>)	Monogamy	64.6	45.2	7.3	12.1	20.9 (20.9)	6.0	12.8
Pectoral Sandpiper (<i>C. melanotos</i>)	Polygyny	72.4	47.1	10.3	15.0	86.0 (60.0)	9.9	23.1
Dunlin (<i>C. alpina</i>)	Monogamy	68.3	45.6	8.9	13.8	54.7 (59.6)	7.8	28.2

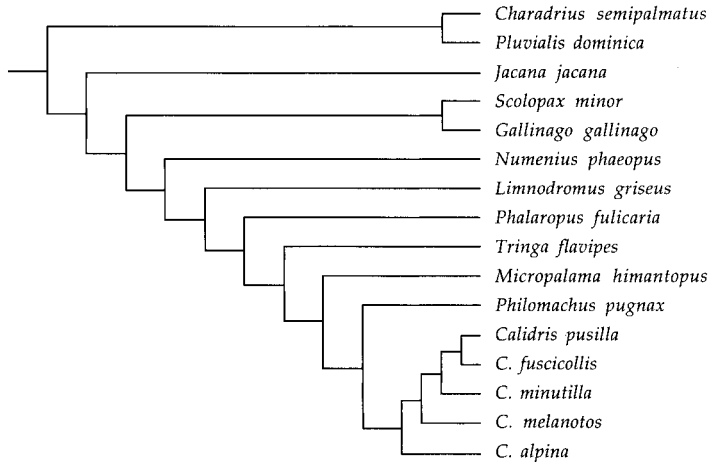


FIGURE 1. Phylogeny for the 16 species of shorebirds examined in this study.

or linkage disequilibrium with egg size. Instead, our results suggest that sperm morphology varies according to the intensity of sperm competition and that those species experiencing the most intense sperm competition (as measured by social mating system and relative testis size) have evolved sperm that are longer in total length and in the length of their component parts.

Few comparative studies of sperm morphology have examined variation among the component parts of a sperm. Gage (1998) recently compared head, midpiece, and tail size across a wide variety of mammals. As with our study, he found a positive correlation between midpiece and tail length. Midpiece size might be expected to vary with tail length as it houses the mitochondria necessary to power the myosin and actin filaments in the flagellum (Cardullo and Baltz 1991, Gage 1998). However, whether the increase in midpiece size is enough to compensate for a larger tail is not known. Gage (1998) did not find a significant correlation between tail length and the volume of the mitochondrial sheath (a more direct measure of energy supply), which suggests that the reason for correlations between midpiece length, tail length, and the intensity of sperm competition may not be entirely energetic. Detailed studies of the number and size of mitochondria, tail structure, and swimming speed are needed to determine how mobility scales with sperm size in shorebirds.

We found that total sperm length, as well as the length of the midpiece and tail, was significantly longer in socially nonmonogamous species than in socially monogamous species of shorebirds. Nonmonogamous species of primates and rodents also have longer sperm than monogamous species (Gomendio and Roldan 1991). Although we used social mating system as a measure of the intensity of sperm competition, social mating associations are not necessarily a measure of the true intensity of sperm competition. This is because females of monogamous species often seek extra-pair copulations (Burke et al. 1989). To avoid this problem we compared sperm size to relative testis size. Although relative testis size is correlated with the level of extra-pair paternity across species (Møller and Briskie 1995), it too may be confounded by the degree of polygyny (Carter 1985). The best measure of sperm competition intensity is the frequency of extra-pair copulations, but such data are not available for most of the species in this study. Nonetheless, the correlations we found between sperm size and both social mating system and relative testis size support the hypothesis that sperm competition has played a part in the evolution of sperm morphology in this group of birds.

A number of studies have now confirmed that sperm size is greater in species with more intense sperm competition (Gomendio and Roldan 1991, Briskie and

TABLE 2. Mean length of sperm components in socially monogamous and nonmonogamous species of shorebirds. Values are means \pm SE.

Length (μm)	Monogamous	Nonmonogamous	p^a
Total	63.5 \pm 1.2	90.2 \pm 8.8	<0.01
Tail	45.2 \pm 1.2	60.7 \pm 5.5	<0.01
Midpiece	7.2 \pm 0.5	15.5 \pm 3.0	<0.01
Head plus acrosome	12.4 \pm 0.6	19.7 \pm 3.8	0.03
n	9	7	

^a Two-tailed t -test on \log_{10} transformed data.

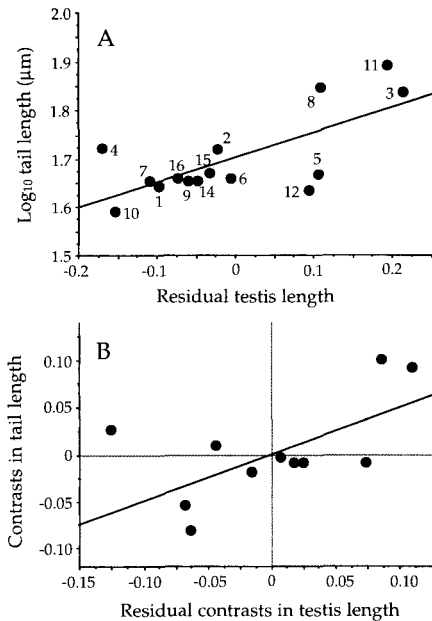


FIGURE 2. Relation between sperm tail length and residual testis length (A) across 15 species of shorebirds, and (B) independent contrasts for these variables, controlling for phylogeny. Numbers refer to species listed in Table 1.

Montgomerie 1992, Gage 1994, 1998), but it is less clear why increased length is advantageous in such situations. In mammals, preliminary evidence indicates that long sperm swim at higher velocity than in species with shorter sperm (Gomendio and Roldan 1991). If speed is an important determinant of fertilization success, then increased sperm length could be a function of selection to increase swimming speed. However, a similar relationship between sperm length and swimming speed is not found in passerine birds (T. R. Birkhead, pers. comm.) and so this explanation appears unlikely to explain the evolution of elongate sperm in shorebirds.

Unlike most mammals, female birds store sperm for extended periods in specialized sperm storage tubules (SSTs; Briskie and Montgomerie 1993). Storage is necessary for the long-term survival of sperm in the female reproductive tract, and it seems likely that storage plays a critical role in the evolution of sperm morphology as several studies have found a strong correlation between sperm length and the length of the SSTs (Birkhead and Møller 1992, Briskie and Montgomerie 1992, 1993). Using a path analysis to identify causal relationships, Briskie et al. (1997) suggested that differences in the intensity of sperm competition were driving changes in SST length and that sperm length was only indirectly related to the level of sperm competition through tracking these changes. The morphology of SSTs in shorebirds is currently under study (J. V. Briskie and R. Montgomerie, unpubl. data), but we predict that the differences we observed in sperm mor-

phology between socially monogamous and nonmonogamous species should likewise be reflected in differences in the pattern of sperm storage by females.

Apart from comparative studies of sperm storage, experimental work also is needed to quantify the hydrodynamic properties of sperm, and how differences in the size of each component affect sperm swimming ability. In this study we assumed that increased mid-piece size was associated with greater resources devoted to motility, but it is unknown how variation in the size of this structure influences the hydrodynamics of sperm with differing tail lengths. Although we found that variation in sperm length of shorebirds was best explained by sperm competition intensity, the adaptive significance of this pattern is uncertain. A key to answering this problem may lie in integrating empirical studies of the fine ultrastructure of sperm with broader scale observations of how sperm are stored prior to fertilization in species with differing sperm morphology.

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GENETIC MONOGAMY IN LONG-EARED OWLS¹

JEFFREY S. MARKS

Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812,
e-mail: jmarks@selway.umt.edu

JANIS L. DICKINSON AND JOSEPH HAYDOCK

Hastings Natural History Reservation and Museum of Vertebrate Zoology, University of California,
38601 East Carmel Valley Road, Carmel Valley, CA 93924

Abstract. We used DNA fingerprinting to study genetic parentage in socially monogamous Long-eared

Owls (*Asio otus*). We detected no extra-pair fertilizations (EPFs) in 59 nestlings from 12 nests. One of these nests was solitary, but the other 11 had from one to five pairs of owls nesting simultaneously within 30 to 250 m. Thus, despite the presumably high potential

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