

What is the relative importance of sexual selection and ecological processes in the evolution of sexual size dimorphism in monogamous shorebirds?

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Three major groups of hypotheses have been proposed to account for the evolution of sexual size dimorphism in animals: sexual selection, intersexual competition and ecological role division. I evaluate two hypotheses for the female-biased sexual size dimorphism (females larger than males) of socially monogamous shorebirds. The *aerial agility hypothesis* is based on sexual selection. It argues that small-bodied males obtain greater mating success because mate choice is based on aerial displays and agility is greater if body size is small. I propose a new hypothesis based on ecological role division: the *differential migration hypothesis*. This argues that long-distance movements could lead to sexual differences in optimal body size if the sexes differ in the timing of their migratory movements or their nonbreeding distributions. I test these hypotheses by re-evaluating results from two published studies.

In a population study of Western *Calidris mauri* and Semipalmated Sandpipers *C. pusilla*, I previously reported little evidence for disassortative mating (i.e. large-bodied females pairing with small-bodied males) and size-dependent reproductive performance (Sandercock 1998). In the present paper, I find that my original conclusions are unchanged if I control for: *i*) the potential effects of relative age on body size, and *ii*) the effects of site- and mate-familiarity on breeding performance.

Population studies of shorebirds provide only weak evidence for the aerial agility hypothesis; no study has yet linked reproductive success to body size *and* body size to agility. Studies that have compared shorebirds in a phylogenetic context provide some of the strongest tests of hypotheses for the evolution of sexual size dimorphism. Figuerola (1999) published a phylogeny of monogamous shorebirds that included information on sexual size dimorphism and presence of acrobatic displays. I categorized the same set of species as being latitudinal migrants, partial migrants or mainly resident species. I found that the Scolopacine clade was invariant for these traits: all 21 species had female-biased dimorphism, acrobatic aerial displays by males and were latitudinal migrants. This pattern is consistent with both the aerial agility and differential migration hypotheses. Variation in the Charadrine clade, however, supported only the aerial agility hypothesis. The balance of evidence from comparative analyses favours sexual selection as the most likely explanation for female-biased size dimorphism in monogamous shorebirds. However, ecological processes may also be important. They have received little attention to date as potential explanations for the evolution of sexual size dimorphism in shorebirds, and I offer recommendations for future studies.

INTRODUCTION

Sexual size dimorphism is widespread among animals; males are larger than females in most birds and mammals whereas the opposite is true among invertebrates, amphibians and reptiles (Andersson 1994, Fairbairn 1997). These taxonomic differences have influenced the terminology and prevailing hypotheses for dimorphism. Although sexual size dimorphism is often described as “normal-” or “reversed-” by ornithologists, a broader taxonomic perspective indicates that “male-biased” and “female-biased” dimorphism are more appropriate terms.

Size dimorphism is often attributed to a selective pressure on one sex: sexual selection on males among male-biased species versus a fecundity-advantage of large female size in

female-biased species (Shine 1988, 1989). Arak (1988) noted that the evolution and maintenance of sexual size dimorphism should be viewed as the net balance between the selective pressures on body size in both females and males. Evolution of sexual size dimorphism is likely to occur slowly because selective pressures on body size must overcome genetic correlations between the sexes that are often high (e.g., $r > 0.95$, Lande 1980, Merila *et al.* 1998).

Three groups of hypotheses have been proposed to explain the evolution of sexual size dimorphism in animals: sexual selection, intersexual competition for food and ecological role division (Hedrick & Temeles 1989, Shine 1989, Table 1). Sexual selection emphasizes the importance of mate choice and competition among individuals of the same sex. In contrast, intersexual competition for food and ecological role



Table 1. Hypotheses for the evolution of female-biased sexual size dimorphism in monogamous shorebirds.

Description of hypotheses		Stage of annual cycle	Predictions for comparative analyses
Sexual selection	<i>Aerial agility hypothesis:</i> Females prefer to mate with small bodied males that are acrobatic in aerial courtship displays.	Breeding (mate choice)	Female-biased dimorphism in species with acrobatic flight displays.
	<i>Fecundity advantage hypothesis:</i> Males prefer to mate with large-bodied females that breed earlier or produce large yolk-rich eggs.	Breeding (egg production)	Female-biased dimorphism in species breeding in harsh conditions, such as high latitudes.
Intersexual selection	<i>Intersexual selection hypothesis:</i> Ecological competition between the sexes for food or other resources leads to sexual size dimorphism.	Breeding, Migration or Nonbreeding	Dimorphism greatest in species with biparental care of young.
			Dimorphism greatest in species where nonbreeding areas of the sexes overlap.
Ecological	<i>Flight efficiency hypothesis:</i> Sex roles are specialized during the nesting cycle. Dimorphism influences parental contributions to nest defence and provisioning of young.	Breeding (incubation or care of young)	Dimorphism greatest in species with biparental care of young.
	<i>Parental role hypothesis:</i> Large-bodied females produce larger eggs; small-bodied males are more efficient at foraging in terrestrial habitats and providing parental care after hatching.	Breeding (care of young)	Dimorphism greatest in species with uniparental care of young.
	<i>Differential migration hypothesis:</i> The sexes migrate at different times and use separate nonbreeding areas. Selection regimes of dissimilar ecological conditions lead to dimorphism.	Migration or Nonbreeding	Dimorphism greatest in species where nonbreeding areas of the sexes are separated.

division include hypotheses that emphasize the potential importance of ecological processes. Of these ideas, sexual selection has received the most attention, in part because critical tests of hypotheses based on ecological processes are difficult to devise (Shine 1989). Jehl & Murray (1986, 1989) have argued that sexual selection is the sole determinant of the direction of size dimorphism in shorebirds, and that ecological processes act secondarily, if at all, to modify the magnitude of dimorphism. Elsewhere, this view has been accepted to the extent that sexual dimorphism is sometimes used as an index of sexual selection itself (refs. in Burns 1998). Studies of sexual size dimorphism might gain insights from a more holistic viewpoint, and several recent studies have considered the combined effects of sexual selection and ecological processes (Webster 1997, Figuerola 1999, Moorhouse *et al.* 1999).

Shorebirds are an excellent group for testing hypotheses about the evolution of sexual size dimorphism because size and plumage variation between the sexes in shorebirds nearly spans the full range found in all birds. The objectives of this paper are threefold: *i*) to review hypotheses for the evolution of sexual size dimorphism, *ii*) to propose a new hypothesis for evolution of sexual size dimorphism, and *iii*) to present two re-analyses that are relevant to these hypotheses in socially monogamous shorebirds.

HYPOTHESES FOR EVOLUTION OF SEXUAL SIZE DIMORPHISM

Sexual selection

Sexual selection via competition for access to mates or mate choice should lead to sexual size dimorphism if variation in reproductive success is related to variation in body size.

Sexual selection has clearly been important in shorebirds because sexual size dimorphism is related to both mating system and parental care (Jönsson & Alerstam 1990, Székely *et al.* 2000). Ecological processes are potentially relevant because polygamous species are more likely to be long-distance migrants and breed later in the season than monogamous species (Myers 1981a, Whitfield & Tomkovich 1996). The relative importance of sexual selection and ecological processes is less clear in socially monogamous species, many of which have female-biased size dimorphism.

Jehl & Murray (1986) proposed the *aerial agility hypothesis* to account for female-biased size dimorphism in monogamous shorebirds with acrobatic courtship displays. If mate choice is based on aerial displays and agility is inversely related to body size, small-bodied males may have greater mating success. An agility advantage of small body size could potentially benefit either sex. However, the *fecundity-advantage hypothesis* suggests that optimal body size will differ between the sexes if males prefer to mate with large-bodied females that improve the survival of their precocial young by breeding earlier or producing larger eggs (Summers & Underhill 1991, Sandercock 1998). Sexual selection predicts that dimorphism should be greatest in the sexual traits used in competition for mates and mate choice.

Intersexual competition

Ecological competition between the sexes for food is a disruptive selection pressure that can enhance sexual size dimorphism. The *intersexual competition hypothesis* is supported by a relationship between dimorphism and diet in raptors (Newton 1979), and the dimorphism of bill size and sex-specific foraging niches of many wood-probing birds (Selander 1966, Suhonen & Kuitunen 1991, Hunt & McLean



1993, Moorhouse *et al.* 1999). In shorebirds, intersexual competition for food and roosting sites during winter is thought to influence the female-biased sexual size dimorphism of Purple Sandpipers *Calidris maritima* (Burton & Evans 2001). Sexual differences in foraging are often viewed as a secondary consequence of size differences resulting from sexual selection (Aulén & Lundberg 1991, Webster 1997), but this interpretation is difficult to reconcile with cases where size dimorphism is female-biased (Hunt & McLean 1993, Moorhouse 1996) or social systems where sexual selection processes seem weak (Moorhouse *et al.* 1999). Intersexual competition predicts that dimorphism should be greatest in the feeding apparatus (bill-size in shorebirds) but it makes no prediction about whether the feeding apparatus of males should be larger than in females or vice versa (Jehl & Murray 1986, 1989, Shine 1989).

Ecological role division

Sexual differences in body size or morphology could also arise if the sexes are adapted to different ecological niches. The *flight efficiency hypothesis* was proposed to explain the female-biased size dimorphism of raptors (Andersson & Norberg 1981). Flight efficiency is dependent on mass and wing morphology (Hedenström & Møller 1992). Small body size may facilitate prey capture by males, whereas defence of offspring and an ability to take larger prey may select for large body size in females. This hypothesis could be relevant to monogamous shorebirds that provision their young or have joint defence of offspring (Larsen *et al.* 1996).

The *parental role hypothesis* combines sexual differences in foraging efficiency and parental care to explain the female-biased dimorphism of monogamous shorebirds (Jönsson 1987). In monogamous sandpipers, females produce eggs, incubation is shared, and males provide most parental care post-hatching (Jönsson & Alerstam 1990, Gratto-Trevor 1991). A fecundity-advantage may lead to selection for large body size in females whereas specialization for feeding in terrestrial habitats during brood-rearing may favour a shorter bill and possibly smaller body size in males.

Here, I propose a new hypothesis based on an alternative evolutionary sequence: the *differential migration hypothesis*. This argues that long-distance movements could lead to sexual differences in optimal body size if females and males differ in the timing of their migratory movements or in their nonbreeding distributions. Long-distance movements lead to selection for efficiency of flight, and migratory birds often have narrower, more pointed wings compared with sedentary species (Mönkkönen 1995). Early return to the breeding grounds is thought to be advantageous for the sex that competes for mates: males in most socially monogamous species, and females in species with sex-role reversal. Small body size could favour more rapid movements to breeding areas by males if flight speed or range were increased, or duration of stopover reduced. For example, male Western Sandpipers *Calidris mauri* have faster rates of mass gain at stopover sites than females (Warnock & Bishop 1998). Females often follow males north during spring migration and could be exposed to different ecological conditions as a consequence (Gauthreaux 1982). Prey depletion occurs at the stopover sites used by shorebirds during spring migration (Székely & Bamberger 1992), so a long bill could help females to access prey items that are unavailable to males. Furthermore, males and females often winter at different

latitudes (Myers 1981b, Gauthreaux 1982, Harrington & Haase 1994) where they may be exposed to different regimes of climate, prey availability, predation risk or interspecific competition (Castro *et al.* 1992, Hockey *et al.* 1992, Cresswell 1994).

The differential migration hypothesis contains elements of sexual selection because it assumes that early return has fitness consequences. It differs from the flight efficiency and parental role hypotheses in that it does not rely on a fecundity-advantage for large female size. As applied to monogamous shorebirds, the differential migration hypothesis predicts that dimorphism was initially generated by ecological processes and that acrobatic courtship displays have evolved as a secondary consequence.

Predictions of hypotheses

Two complementary approaches have been used to test hypotheses for the evolution of sexual size dimorphism in shorebirds (Table 1). Population studies of single species have examined the operation of selection in contemporary populations over ecological time scales. Most have sought to verify the underlying mechanisms of a particular hypothesis. Comparative studies address the same hypotheses in a phylogenetic context and over evolutionary time scales. Most of the hypotheses for the evolution of female-biased sexual size dimorphism in monogamous shorebirds are based on selective forces that operate during the breeding season (Table 1). Many shorebirds spend considerable time away from their breeding areas, and the intersexual selection and differential migration hypotheses are appealing because they shift attention to ecological conditions encountered during migration and the nonbreeding season. Exclusive predictions are not always possible because the six hypotheses emphasize events at different stages of the annual cycle. However, the differential migration hypothesis predicts greater dimorphism in species where the nonbreeding areas of the sexes are separate; the intersexual selection hypotheses predicts greater dimorphism if the nonbreeding ranges overlap.

METHODS AND RESULTS

Population study

Western *Calidris mauri* and Semipalmated Sandpipers *C. pusilla* were studied near Nome, Alaska, during 1993 to 1996. The study site and field methods are described by Sandercock *et al.* (1999, 2000). Previously, I concluded that sexual selection was unimportant in Western and Semipalmated Sandpipers because I found little evidence for size-dependent reproductive performance or disassortative mating in these species (Sandercock 1998). These analyses could have been misleading if body size covaried with sandpiper age (Cooch *et al.* 1992), or if familiarity with a mate or breeding site influenced reproductive performance (Jehl 1973, Sandercock *et al.* 1999). To address these two problems, I reanalysed my data to control for age and experience of sandpipers. Data from the first year of study were discarded and analyses were based on records from 1994 to 1996. Analyses were conducted with procedures of Program SAS (ver. 8).

First, I compared body size among sandpipers that were first captured as naïve breeders and again in a subsequent year. Culmen, tarsus and wing chord did not change with



Table 2. Linear regression analyses of the relationship between residual timing of laying (dependent variable) and body size (PC1, independent variable) in newly paired Western and Semipalmated Sandpipers. Data were pooled 1994 to 1996, but individuals were included once only in the regression analyses. Negative slopes indicate earlier nesting by large-bodied birds.

Species	Familiarity with study area	r^2	Slope \pm 1SE	t	$P \leq$	
Western	Females	Naïve $n = 49$	0.039	-1.39 \pm 1.02	-1.37	0.177
		Experienced $n = 49$	0.007	-0.64 \pm 1.11	-0.57	0.569
	Males	Naïve $n = 47$	0.004	-0.63 \pm 1.42	-0.44	0.662
		Experienced $n = 39$	0.004	-0.54 \pm 1.36	-0.40	0.692
Semipalmated	Females	Naïve $n = 25$	0.088	-2.22 \pm 1.49	-1.49	0.150
		Experienced $n = 30$	0.006	-0.35 \pm 0.83	-0.42	0.676
	Males	Naïve $n = 21$	0.058	-1.93 \pm 1.78	-1.09	0.291
		Experienced $n = 29$	0.016	-0.80 \pm 1.20	-0.67	0.508

relative age among females or males in either species (effect size $< \pm 1.6\%$, paired t -tests, $P > 0.05$). Second, I re-examined the size-dependent reproduction of sandpipers. Familiarity with a mate was eliminated as a factor by restricting the sample to sandpipers with newly formed pair bonds. Naïve pairs consisted of pairs where both members were newly captured and presumed to be unfamiliar. Experienced pairs included at least one bird that had bred on the study area before and was known to have changed mates from the previous year. The potential effect of familiarity with the breeding site was handled by conducting analyses separately for naïve and experienced pairs. Timing of laying differed among years, and laying dates were standardized by subtracting the median laying date for that species in a given year. Residual laying date was the only dependent variable considered because it is strongly correlated with egg size and clutch size in both Western and Semipalmated Sandpipers (Sandercock *et al.* 1999). Laying date was presumed to be correlated with fitness but the exact nature of this relationship was unknown. Good estimates of juvenile survival are rare for shorebirds because population studies are often conducted on small-scale study plots and the young disperse great distances (Sandercock & Gratto-Trevor 1997). Linear regression of timing of laying on a multivariate measure of body size (PC1 from principal components analysis) revealed negative slopes that were not significantly different from zero (Table 2). This result is contrary to the male agility and the differential migration hypotheses which both predict that small-bodied males should breed earlier and the relationship should be positive.

Comparative study

Figuerola (1999) examined the sexual size dimorphism of socially monogamous shorebirds in a phylogenetic context. He presented a phylogeny of monogamous shorebirds with three clades (two species of seedsnipes, 21 species of Scolopaci and 13 species of Charadrii), and used independent contrasts to investigate the patterns of sexual size dimorphism. Detailed information on sex-specific nonbreeding latitudes is unavailable for most shorebirds. To test the differential migration hypothesis, I extended the analyses of Figuerola (1999) by including supplementary information on migratory movements. Using the maps and species descriptions of Hayman *et al.* (1986), shorebird species were scored as: *i) latitudinal migrants* if breeding and nonbreeding areas were clearly separated for all populations, *ii) partial migrants*

if migrant and resident populations were common within the species, or *iii) resident* if most populations were not latitudinal migrants. This approach assumes a negative correlation between migration distance and the degree of overlap between the nonbreeding distributions of females and males.

The two seedsnipes are monomorphic, do not have acrobatic displays and are both resident species (Figure 1). Intriguingly, the 21 Scolopacine species were also invariant for the three characters examined. All 21 species have female-biased size dimorphism, acrobatic aerial displays and latitudinal migratory movements. Thus, the aerial agility hypothesis and the differential migration hypothesis are equally parsimonious explanations for variation in sexual size dimorphism in these two clades. In the Charadriine clade, however, only the aerial agility hypothesis was supported. The two species of Oystercatchers with female-biased sexual size dimorphism were the only species with acrobatic aerial displays. Four species were migratory but only one of these had female-biased dimorphism (Eurasian Oystercatcher). Contrary to the differential migration hypothesis, three migrants were monomorphic or had male-biased dimorphism (Ringed Plover, Eurasian Golden Plover, Pied Avocet), and one resident species had female-biased dimorphism (Variable Oystercatcher).

DISCUSSION

Investigations of female-biased sexual size dimorphism in monogamous shorebirds have focused primarily upon the role of sexual selection. The strength of support for hypotheses based on sexual selection differs between population and comparative studies. A fecundity advantage of large body size has been demonstrated for females of some species, where large-bodied individuals breed earlier or lay larger eggs (Summers & Underhill 1991, Sandercock 1998). To the best of my knowledge, however, no study of a shorebird has reported a male mating preference for large-bodied females. Population studies of monogamous shorebirds generally offer little or no support for the aerial agility hypothesis. In my study of Western and Semipalmated Sandpipers, the aerial agility hypothesis was not supported because small-bodied male sandpipers did not breed earlier. My 4-year observational study is a relatively weak test of the aerial agility hypothesis because I did not address the possibility that small-bodied males are more likely to obtain a mate or extra-pair fertilizations (EPFs). Failure to obtain a mate and EPFs are rare in arctic-breeding sandpipers (Jehl 1973,



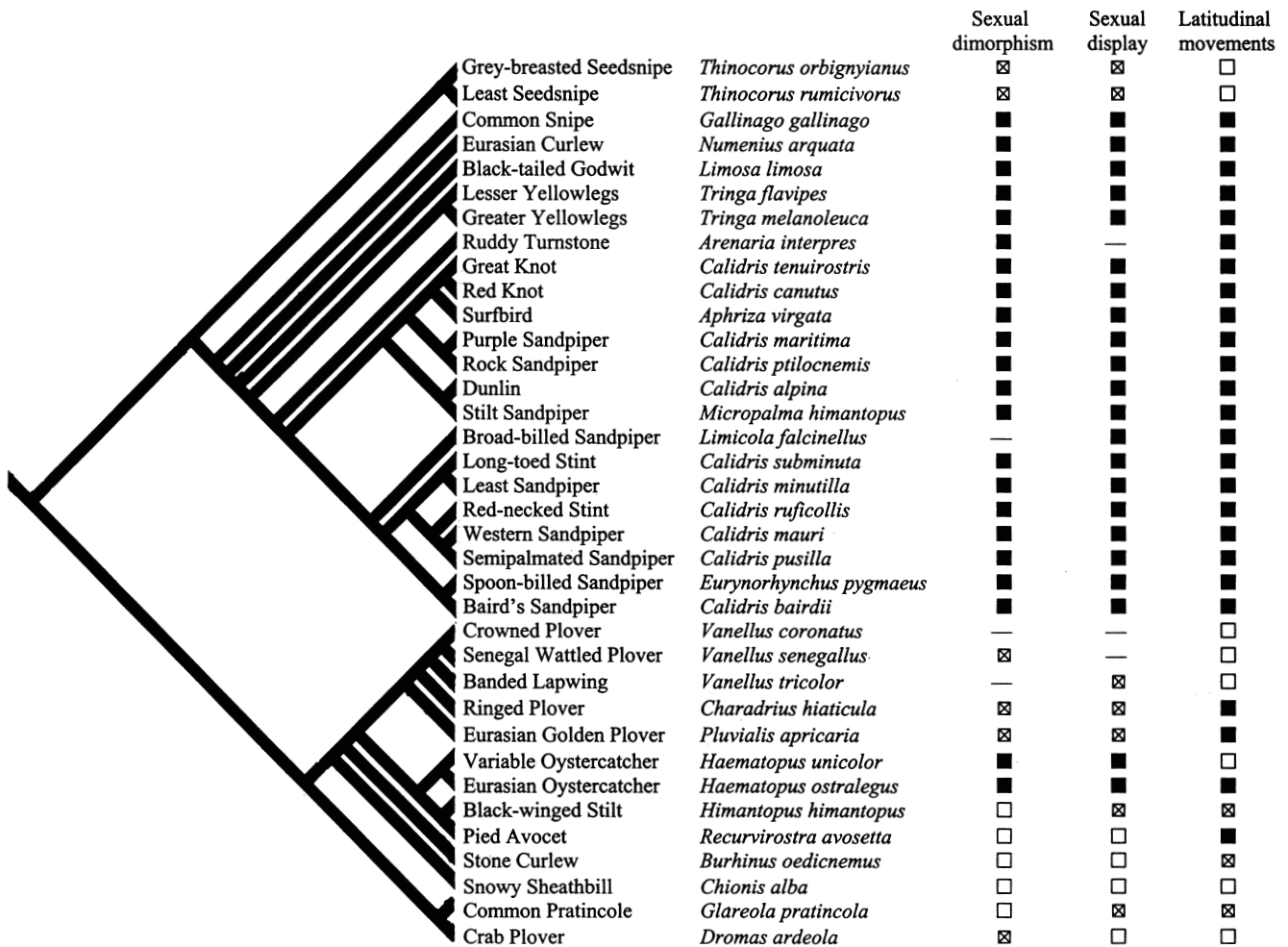


Figure 1. Sexual size dimorphism, sexual displays and latitudinal movements of socially monogamous species of shorebirds. The shorebird phylogeny and categories of sexual size dimorphism (■ = female-biased, ☒ = monomorphic, ☐ = male-biased) and sexual display (■ = acrobatic flight display, ☒ = nonacrobatic flight display, ☐ = no aerial display) were taken directly from Figuerola (1999). This paper presents new information on latitudinal movements (■ = long-distance migrant, ☒ = partial migrant, ☐ = resident). Migration categories were scored using information in the species descriptions of Hayman *et al.* (1986).

Gratto-Trevor 1991, Pierce & Lijfeld 1998, Blomqvist *et al.* in press), but these aspects of reproductive performance have not been related to body size for any shorebird.

In previous population studies, evidence for the aerial agility hypothesis was based on patterns of size-dependent reproductive success and disassortative mating. Jehl (1970) and Jönsson (1987) claimed evidence that small males paired to large females bred earlier, possibly obtaining higher reproductive success. I have argued that the conclusions of these studies are equivocal because questionable statistical methods were used (Sandercock 1998). Blomqvist *et al.* (1997) reported correlations between tarsus length and aspects of aerial courtship display in a small sample ($n = 11$) of male Dunlin *C. alpina*, but did not relate agility to reproductive performance. Grønstøl (1996) and Liker & Székely (1999), on the other hand, showed that mating success is related to features of song-flights in male Lapwings *Vanellus vanellus*, but provided no data linking aerial courtship displays to male body size. While the results of these studies are suggestive, no population study can claim observational or experimental evidence that links shorebird body size to agility and agility to fitness.

The aerial agility hypothesis predicts that dimorphism

should be greatest in structural traits that affect wing loading (Mueller 1989). Contrary to the aerial agility hypothesis, culmen length is generally more dimorphic than other structural traits of shorebirds (Jehl & Murray 1986). Sexual selection processes could be relevant if mate choice was based on bill morphology (Mueller 1989), but this seems unlikely for most monogamous shorebirds, with the possible exception of oystercatchers (Lauro & Nol 1995). On the other hand, sexual differences in foraging behaviour are widespread in shorebirds (Puttick 1981, Townshend 1981, Durell *et al.* 1993, Pierre 1994, Lauro & Nol 1995, Durell 2000). Thus, it seems plausible that intersexual competition or ecological role division could explain some of the variation in the magnitude if not the direction of size dimorphism.

Early reviews of dimorphism in shorebirds were published before comparative methods became widely available (Jehl & Murray 1986, Jönsson & Alerstam 1990). The independent contrasts used by Reynolds & Székely (1997), Figuerola (1999) and Székely *et al.* (2000) offer some of the strongest tests of hypotheses for the evolution of female-biased size dimorphism in monogamous shorebirds because they incorporate phylogenetic relationships into their statistical analyses. The latter two studies demonstrated a strong



concordance between female-biased dimorphism and acrobatic displays, supporting the aerial agility hypothesis.

Still, the potential importance of intersexual selection and ecological role division has received relatively little attention. Reynolds & Székely (1997), Figuerola (1999), and Székely *et al.* (2000) did not consider variation in diet, tendency to migrate or differential migration in their comparative analyses. The extended analyses of the present paper are one of the first attempts to examine the role of ecological processes. It is intriguing that many of the species with female-biased sexual size dimorphism are also long-distance migrants, especially among the Scolopaci (Figure 1). However, variation in dimorphism within the Charadrii clade was more consistent with the aerial agility than the differential migration hypothesis. In other tests, Figuerola (1999) found that migration distance did not differ between acrobatic and non-acrobatic species. Székely *et al.* (2000) found that species with biparental care of young did not have greater dimorphism in bill length than species with uniparental care, contrary to the parental role hypothesis. Overall, the balance of evidence from comparative analyses favours sexual selection as the most likely explanation for female-biased sexual size dimorphism in monogamous shorebirds.

Recommendations for future studies

Future studies of female-biased sexual size dimorphism in monogamous shorebirds should proceed in several directions. First, population studies could provide better tests of the aerial agility hypothesis. This hypothesis would be bolstered by an experimental study of a single species that demonstrated that small males are more agile and that agile birds obtain greater reproductive success. Given that many shorebirds spend the majority of their annual cycle in nonbreeding areas, population studies should examine selection regimes that act on body size outside the breeding season. The differential migration hypothesis introduced here is one of the first attempts to shift focus to this part of the annual cycle.

Second, comparative studies could do more to include ecological factors in their analyses. A better test of the differential migration hypothesis could examine sexual differences in nonbreeding distributions and timing of migration as better information becomes available for more species. The results of parsimony analyses can be sensitive to choice of the sample set of taxa and an appropriate outgroup. The present analyses and Figuerola (1999) were restricted to monogamous shorebirds; results might change if the differential migration hypothesis was tested across a broader range of taxa. Current phylogenetic hypotheses for some shorebird genera are best viewed as provisional (e.g., *Calidris*, Baker 1992, Borowik & McLennan 1999), and all comparative analyses should be revisited as alternative phylogenies are published.

Last, it could be profitable if the focus of future studies was expanded to test the same hypotheses with additional traits and in different groups of birds. Body size is one trait that sexual selection and ecological processes act upon, and sexual variation in shorebird plumage and vocalizations could be considered as well. It is curious that some godwits *Limosa* spp. have female-biased sexual size dimorphism but males are the brighter sex. Breeding vocalizations are poorly developed in the Ruff *Philomachus pugnax*. Could this be a partial explanation for their pronounced sexual differences in body size and plumage? Additional insights could also be

gained from other avian lineages. Some songbirds also have acrobatic courtship displays, but contrary to the aerial agility hypothesis, many of these species have male-biased sexual size dimorphism (e.g., Greenfinch *Carduelis chloris*; Hedenström & Møller 1992, Andersson 1994). Future studies would be prudent to consider alternative hypotheses for the evolution of sexual dimorphism, as well as the possibility that these processes may be acting in concert.

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