

# Directional changes in sexual size dimorphism in shorebirds, gulls and alcids

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## Abstract

The Charadrii (shorebirds, gulls and alcids) are one of the most diverse avian groups from the point of view of sexual size dimorphism, exhibiting extremes in both male-biased and female-biased dimorphism, as well as monomorphism. In this study we use phylogenetic comparative analyses to investigate how size dimorphism has changed over evolutionary time, distinguishing between changes that have occurred in females and in males. Independent contrasts analyses show that both body mass and wing length have been more variable in males than in females. Directional analyses show that male-biased dimorphism has increased after inferred transitions towards more polygynous mating systems. There have been analogous increases in female-biased dimorphism after transitions towards more socially polyandrous mating systems. Changes in dimorphism in both directions are attributable to male body size changing more than female body size. We suggest that this might be because females are under stronger natural selection constraints related to fecundity. Taken together, our results suggest that the observed variation in dimorphism of Charadrii can be best explained by male body size responding more sensitively to variable sexual selection than female body size.

## Introduction

Sexual size dimorphism is one of the most prominent manifestations of sexual selection (reviewed by Andersson, 1994; Reynolds & Harvey, 1994; Fairbairn, 1997; Owens & Hartley, 1998). It can take many forms, including differences between males and females in overall body size and/or in the size of a particular part of the body such as ornaments (Cuervo & Møller, 1999; Dunn *et al.*, 2001). Sexual size dimorphism may also be driven by natural selection. For example, differences in parental care by males and females may lead to different structures related to brood-rearing, and habitat differences during the nonbreeding season may lead to sexual dimorphism in structures related to foraging (e.g. Temeles *et al.*, 2000). The interactions between these various selection processes in a contemporary avian

population have been thoroughly demonstrated by Badyaev & Martin (2000) and Badyaev *et al.* (2001).

Researchers usually attribute greater body size in males than in females to sexual selection acting on males (Promislow *et al.*, 1992; Andersson, 1994; Dunn *et al.*, 2001). In other words, dimorphism is often considered as the outcome of evolutionary increases in body size of males as a result of competition for access to females. However, the processes that lead to dimorphism may act on either sex, or they may act on both sexes at different magnitudes. For example, reductions in male size may have produced female-biased dimorphism in spiders (Vollrath & Parker, 1992, 1997; but see also Coddington *et al.*, 1997; Prenter *et al.*, 1999). Similarly, Karubian & Swaddle (2001) argued that male-biased dimorphism has evolved in cardueline finches by reducing female size as opposed to the conventional view of increasing male size. Directional phylogenetic analyses of male and female size evolution separately have proved fruitful when investigating changes in body size that lead to the evolution of sexual size dimorphism (Björklund, 1991; Lindenfors & Tullberg, 1998).

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Charadrii (shorebirds, gulls and alcids) are an excellent group to test hypotheses for the evolution of sexual size dimorphism because they have an exceptional range of dimorphism, encompassing nearly the entire range found in birds. There is also large variation in the potential for sexual selection due to a diversity of mating systems that includes social polygyny, monogamy and polyandry. Furthermore, display behaviour, which is important in the evolution of shorebird dimorphism (Figuerola, 1999; Székely *et al.* 2000), is highly variable in this group. Thus there is ample variation both in size and in forms of selection to cause sexual size dimorphism.

The objective of our study was to test predictions from hypotheses for the evolution of sexual size dimorphism in Charadrii with a focus on temporal changes in dimorphism. Size dimorphism is correlated significantly with the strength of sexual selection as manifested by the intensity of mate competition both between males and between females (Székely *et al.*, 2000), and by the agility of male display behaviour (Figuerola, 1999; Székely *et al.*, 2000). However, whether the correlations between sexual selection and size dimorphism were due to evolutionary changes in male size, in female size, or both, were not tested. This study focuses on each sex separately and uses analyses that examine directions of change over time in order to elucidate the processes that have led to sexual dimorphism in Charadrii.

The expectations from differences in mating systems are that male-biased sexual size dimorphism should have become more pronounced in more socially polygynous species through male size increase, while female-biased dimorphism should have become more pronounced in more socially polyandrous species through female size increase (Andersson, 1994; Székely *et al.*, 2000). For display agility we test the hypothesis that as smaller males may benefit from enhanced manoeuvrability (Andersson & Norberg, 1981; Jehl & Murray, 1986; Blomqvist *et al.*, 1997), transitions towards more acrobatic aerial displays should result in decreased male-biased dimorphism through decreases in male size.

## Materials and methods

We use the data set described by Székely *et al.* (2000). Mating system and display type were treated as categorical variables. Mating system was divided into three states – social polyandry, social monogamy and social polygyny – and display type was categorized as ground display, nonacrobatic aerial display and acrobatic aerial display (see definitions in Székely *et al.*, 2000). Body mass and wing length were  $\log_{10}$  transformed prior to the analyses.  $\log_{10}(\text{male}) - \log_{10}(\text{female})$  was used as an indicator of dimorphism in both body mass and wing length.

Two phylogenetic comparative methods were used in this study: Felsenstein's (1985) independent contrasts analysis, which uses the full phylogenetic hypothesis to

calculate differences between taxa (or nodes), and weighs this difference by the estimated time of divergence, and the common origins test (Lindenfors & Tullberg, 1998) where each data point is the sum of changes in a sub-clade that is defined by a common origin of mating system (or display type).

We used the phylogeny of Székely *et al.* (2000) based on both molecular and morphological data. This composite phylogeny had been assembled from several published phylogenies that have been proposed for various subsets of the Charadrii suborder. As the understanding of the shorebird phylogeny is still in a state of flux, with work in several laboratories currently in progress, we investigated the robustness of our results by also using a purely morphology-based phylogeny of Charadrii (Chu, 1995). Specifically, we tested the influence of mating system and display type on body mass using matched pairs analyses (Møller & Birkhead, 1992; Wickman, 1992). The results of these analyses were fully consistent between the two phylogenies.

## Nondirectional analyses

Independent contrasts analyses (Felsenstein, 1985), as implemented by the computer program PDAP (Garland *et al.*, 1993), were used to investigate the relationship between body mass and wing length of males and females. Branch lengths were set to unity. Prior to using the contrasts method, diagnostics as described by Garland *et al.* (1992) were carried out. As these diagnostics revealed no significant trends in the data no adjustments of the branch lengths were needed.

The contrasts were analysed with major axis regressions through the origin rather than ordinary least-squares regressions because there is no *a priori* reason to allocate either sex to the *x* or *y* variable (Rayner, 1985). To identify which sex has the largest magnitude of change in mass or wing length we calculated 'positivized' contrasts, where one first gives positive signs to all female contrasts, simultaneously switching the sign, if needed, of the male contrasts (Garland *et al.*, 1992). Then we compared the 'positivized' contrasts between sexes using paired tests. The null expectation is that these contrasts are not different between males and females.

## Directional analyses

We used the common origins test (Lindenfors & Tullberg, 1998) to investigate whether size dimorphism was achieved through increases in one sex, decreases in the other, or a combination of these two processes. For this test we used parsimony reconstructions of ancestral states in the categorical variables. As neither mating system nor display type could be assumed to be ordered characters *a priori*, both were treated as unordered.

Ancestral states could not be reconstructed unambiguously in the present study. Instead several equally

parsimonious reconstructions had to be dealt with: 18 and 24 reconstructions of mating system and display type, respectively. As data are missing for some species (see Székely *et al.*, 2000), the sample sizes vary in the common origins tests depending on the reconstruction.

For the continuous variables of body mass and wing length we used linear parsimony reconstructions of ancestral states (Swofford & Maddison, 1987). We also performed squared-change parsimony reconstructions (Maddison, 1991) to investigate the sensitivity of our results to the mode of character reconstruction. The results of the linear and squared-change parsimony reconstructions were fully consistent, and thus we only report the linear ones. We favoured linear parsimony reconstructions over squared-change parsimony reconstructions, because the latter spreads changes from one part of the tree onto neighbouring branches (Maddison, 1991).

Any ambiguity in the linear parsimony reconstructions, however, produces a range of possible values in the ancestor's character state. We therefore included the upper limit of the range, the lower limit of the range and the range mean in our calculations. This yielded 54 and 72 reconstructions for the analyses of mating system and display type, respectively. As the variances of several response variables were heterogeneous, nonparametric tests were used. We present the range of all resulting *P*-values, as well as their mean and standard deviations.

## Results

### Nondirectional analyses

The independent contrasts analysis shows a correlation between evolutionary changes in body mass of males and females (Fig. 1a:  $R^2 = 0.967$ ,  $P < 0.001$ ,  $n = 57$ ). The slope did not differ significantly from 1.000 ( $b = 1.048$ ,

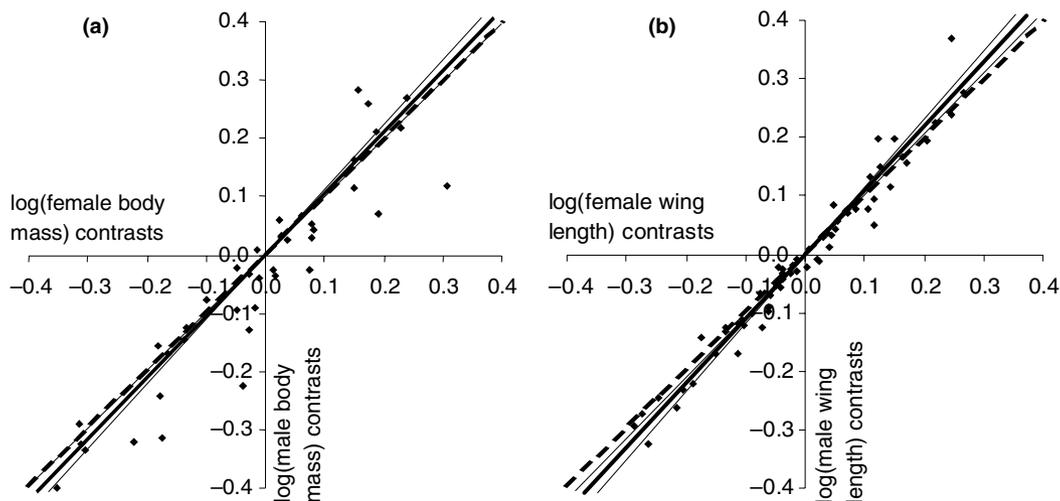
$P > 0.05$ ). With a 'positivized' contrasts analysis, however, we found that changes in male mass were larger than changes in female mass throughout the phylogeny (Wilcoxon's matched pairs,  $P = 0.010$ ,  $n = 57$ ). This result shows that male body mass was more variable over evolutionary time than female body mass.

The evolutionary changes in wing lengths of males and females were also correlated (Fig. 1b:  $R^2 = 0.962$ ,  $P < 0.001$ ,  $n = 63$ ). The slope for wing length is statistically different from 1.000 ( $b = 1.101$ ,  $P < 0.001$ ). Thus, increases and decreases in wing length have entailed corresponding increases and decreases in wing length dimorphism, respectively. As in the case for body mass, a statistical test of the 'positivized' contrasts showed that the wing length is more variable in males than in females throughout the phylogeny (Wilcoxon's matched pairs,  $P = 0.024$ ,  $n = 63$ ).

### Directional analyses

#### Mating systems

Parsimonious phylogenetic reconstructions indicate that the ancestral mating system of shorebirds was social monogamy (Fig. 2). Our reconstruction had 18 transitions in mating system, with eight to 11 transitions to social polygyny, five to seven transitions to social polyandry and zero to five reversals to social monogamy (Fig. 2). All of these transitions were from social monogamy to either social polyandry or social polygyny. Thus, two types of transitions are inferred to have occurred during shorebird evolution: social polyandry  $\leftrightarrow$  social monogamy, and social monogamy  $\leftrightarrow$  social polygyny. All transitions going to the right in this line-up were classified as being transitions towards more polygyny, whereas transitions going to the left were classified as being towards more polyandry. This gives two groups to



**Fig. 1** Major axis regressions through zero (thick lines) on male and female (a) body mass contrasts and (b) wing length contrasts. The 95% confidence intervals (thin lines) include the slope of 1 (dashed lines) for body mass contrasts but not for wing length contrasts.

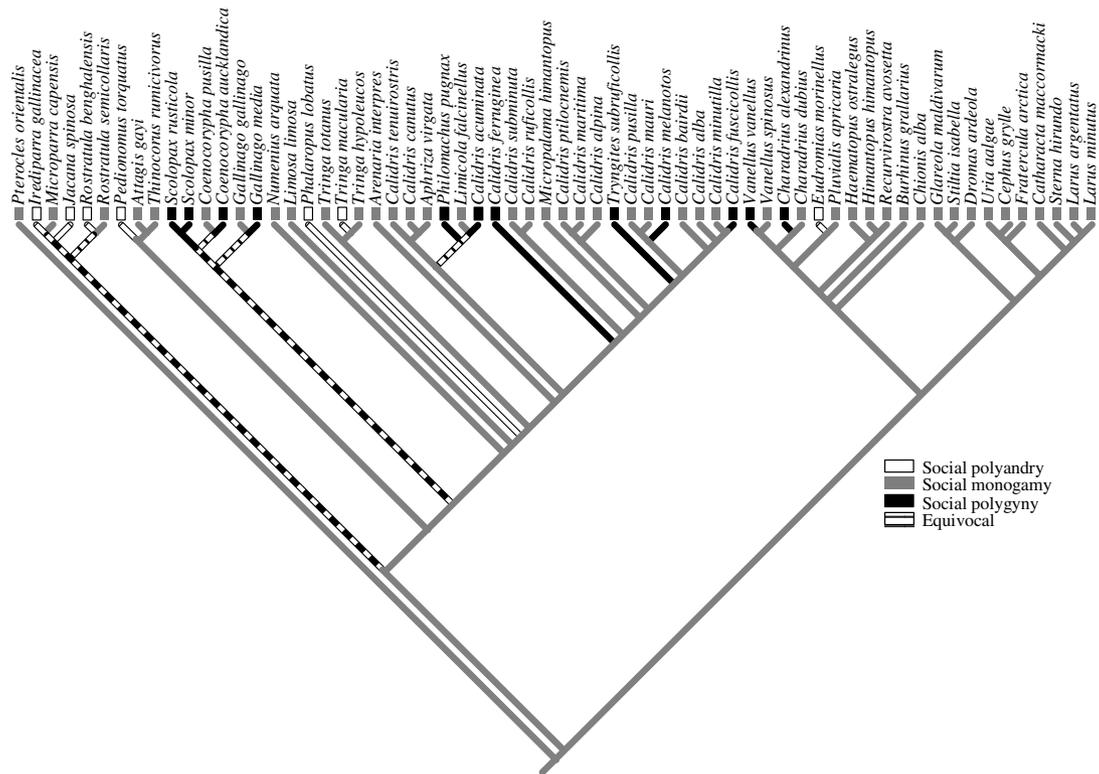


Fig. 2 Phylogeny of Charadrii showing the most parsimonious reconstruction of mating systems.

compare with respect to predicted changes in intensity of competition in each sex, henceforth referred to as 'more polygynous' and 'more polyandrous'.

As predicted, more socially polygynous species have become more male-biased dimorphic when compared with more socially polyandrous species, which instead have become more female-biased dimorphic [Fig. 3a, Mann-Whitney  $U$ -tests:  $\bar{P} = 0.018 \pm 0.011$  ( $0.006 < P < 0.042$ )  $n = 15-18$ ]. Thus, although changes in body mass are tightly coupled between the sexes, they differ enough in magnitude to result in statistically detectable differences in body mass dimorphism. There were no statistical differences in magnitude between changes related to social polygyny when compared with changes related to social polyandry.

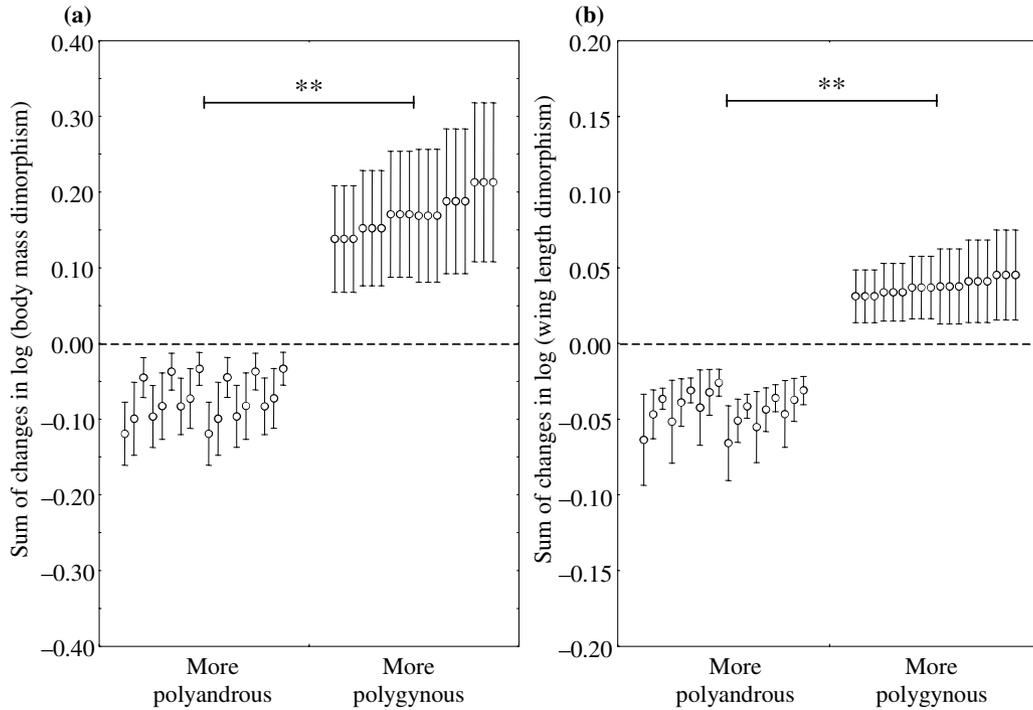
Male-biased wing length dimorphism also increases with increasing social polygyny when compared with female-biased wing length dimorphism, which instead increases with more polyandrous mating systems [Fig. 3b: Mann-Whitney  $U$ -tests  $\bar{P} = 0.014 \pm 0.014$  ( $0.001 < P < 0.077$ )  $n = 18-20$ ]. As was the case for body mass, changes in dimorphism were equally large whether they were correlated with the occurrence of social polygyny or social polyandry.

To attempt to pry apart which sex has changed size, thereby causing the above reported changes in dimorphism, common origins tests were carried out on each sex

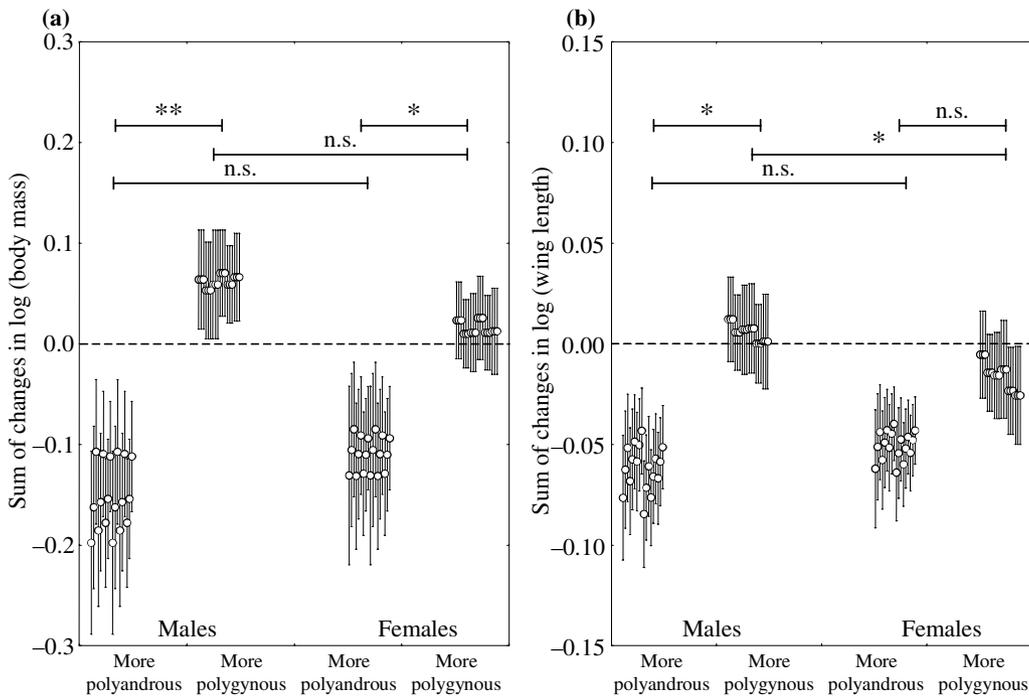
separately. As predicted, transitions towards a more polygynous mating system entailed increases in male body mass, whereas transitions towards a more polyandrous mating system were associated with a decrease in male body mass [Fig. 4a: Mann-Whitney  $U$ -tests comparing the two transitions:  $\bar{P} = 0.013 \pm 0.006$  ( $0.003 < P < 0.028$ )  $n = 15-18$ ]. Contrary to our expectation, females followed the same pattern, i.e. they also became larger in transitions to more polygynous mating systems, whereas their body mass decreased after transitions towards more polyandrous mating systems [Fig. 4a: Mann-Whitney  $U$ -tests comparing the two transitions  $\bar{P} = 0.030 \pm 0.012$  ( $0.013 < P < 0.064$ )  $n = 15-18$ ]. Transitions to social polygyny entailed equally large changes in body mass as did transitions to social polyandry.

Tests on the differences in changes in body mass between males and females within either group (more polygynous or more polyandrous) did not reveal statistically significant differences for most alternative reconstructions [Wilcoxon's matched pairs test, more polygynous:  $\bar{P} = 0.341, \pm 0.319$  ( $0.043 < P < 0.917$ )  $n = 8-11$ ; more polyandrous:  $\bar{P} = 0.281 \pm 0.308$  ( $0.046 < P < 0.917$ )  $n = 5-9$ ]. In those reconstructions in which the differences between the sexes were significant, changes in body mass of males were always larger than those of females.

Evolutionary changes in wing lengths yielded similar patterns to those for body mass (Fig. 4b). Thus,



**Fig. 3** Results from the common origins tests concerning the effects of sexual selection on dimorphism (male:female) in (a) body mass and (b) wing length. Eighteen equally parsimonious reconstructions of mating systems were possible, and thus 18 means  $\pm$  SE are presented in the graphs.



**Fig. 4** Results from the common origins tests concerning the effects of sexual selection on (a) body mass and (b) wing length of males and females. Eighteen equally parsimonious reconstructions of mating systems were possible, and thus 18 means  $\pm$  SE are presented in the graphs.

transitions towards social polygyny brought about increases in male wing length that were different from the wing length changes after transitions towards social polyandry [Mann–Whitney *U*-tests:  $\bar{P} = 0.054 \pm 0.042$  ( $0.007 < P < 0.166$ )  $n = 18$ –20]. The trends for females were similar, although not statistically significant for most alternative reconstructions [Mann–Whitney *U*-tests:  $\bar{P} = 0.246 \pm 0.178$  ( $0.019 < P < 0.705$ )  $n = 18$ –20]. Transitions to social polygyny entailed equally large changes in wing length, as did transitions to social polyandry.

Male wing length increased more than female wing length after transitions towards more polygyny [Fig. 4b: Wilcoxon's matched pairs:  $\bar{P} = 0.021 \pm 0.006$  ( $0.015 < P < 0.028$ )  $n = 8$ –11]. However, there were no unanimous results for the differences between males and females after transitions towards more polyandry [Fig. 4b: Wilcoxon's matched pairs:  $\bar{P} = 0.126 \pm 0.114$  ( $0.028 < P < 0.484$ )  $n = 5$ –9], although in none of the alternative reconstructions did female wing length change more than male wing length.

#### Display types

The ancestral display type was parsimoniously reconstructed as ground display, with a total of 19 transitions: four transitions to acrobatic aerial display, nine to 11 transitions to nonacrobatic aerial display and four to six reversals to ground display. Note that an early transition

to acrobatic aerial display is reconstructed for the Scolopacidae clade, with transitions to the other two states following this event (Fig. 5). Three types of transition were thus possible: ground display  $\Leftrightarrow$  nonacrobatic aerial display, ground display  $\Leftrightarrow$  acrobatic aerial display, and nonacrobatic aerial display  $\Leftrightarrow$  acrobatic aerial display. Transitions going to the right in this line-up were classified as indicating an expected increase in selection for display agility whereas transitions going to the left were classified as indicating an expected decrease in selection for display agility. This gives two groups to compare, 'expected increase' and 'expected decrease' in selection for display agility by males. Note that the two groups – expected increase and expected decrease – do not consist mainly of any specific display type. Treating the transitions in display types as three different entities (to nonacrobatic, to ground, and to acrobatic display) did not give qualitatively different results from treating them as two entities (expected increase and expected decrease), and thus these results are not presented.

The results of the common origins tests show that display type has not had any clear influence on either body mass or wing length (Mann–Whitney *U*-tests: mean *P*-values between 0.233 and 0.582) except a tendency for mass dimorphism to have been affected in the expected direction, i.e. a decrease in male-biased dimorphism after increases in display agility in some of the alternative

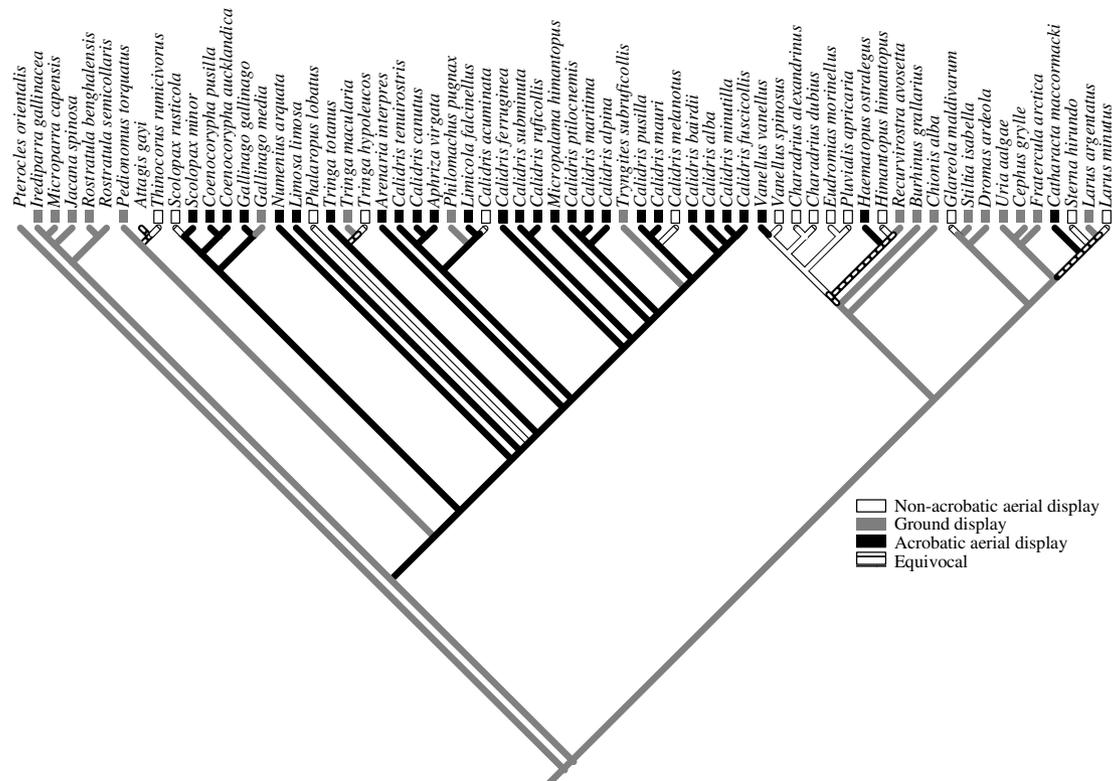


Fig. 5 Phylogeny of Charadrii showing the most parsimonious reconstruction of display type.

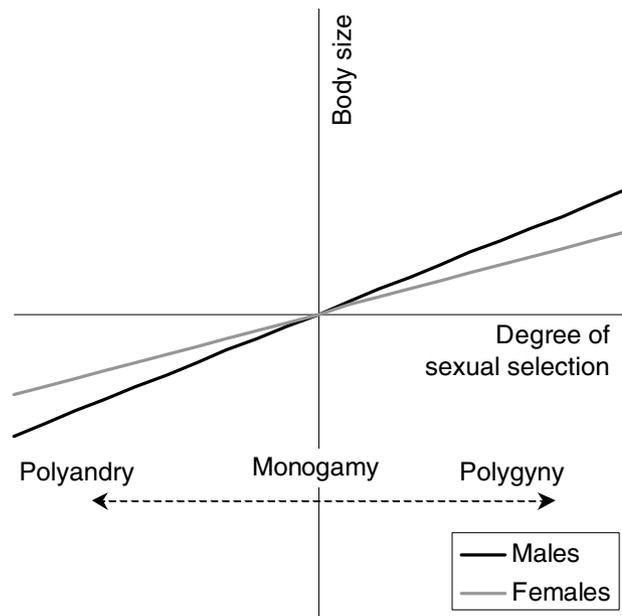
reconstructions [Mann–Whitney  $U$ -tests  $\bar{P} = 0.051 \pm 0.054$  ( $0.006 < P < 0.198$ )].

## Discussion

The analyses presented here are the first to test for directions of change in size dimorphism and in body size of each sex separately in shorebirds, gulls and alcid. The findings support the conclusions of previous nondirectional studies that sexual selection has been a major force behind sexual size dimorphism in this group. Male body size, measured both as body mass and wing length, has been more variable during evolution than female body size. Further, the directional analyses show that male-biased dimorphism has increased as species have moved either from social polyandry to monogamy, or from monogamy to social polygyny. A complementary result is that female-biased dimorphism has increased with transitions towards social polyandry (from polygyny to monogamy or monogamy to polyandry).

To investigate these findings further, each sex was analysed separately. Independent contrasts reveal that the correlation in body size between the sexes is so high that the effects of sexual selection on the sexes separately were difficult to pry apart statistically in the directional analysis. This coupling can be the result of a genetic correlation. It could be argued that this would be a temporary phenomenon occurring before females reach their own optimal size (Maynard Smith, 1978; Lande, 1980, 1987; Lande & Arnold, 1983; Shaw *et al.*, 1995; Merilä *et al.*, 1998). Alternatively, it could result from correlational selection, for instance if larger females produce larger sons (Fairbairn, 1997; Lindenfors, 2002a,b). The pattern of sexual selection causing body size changes for both sexes, but larger changes for males than for females, is similar to the pattern reported for primates (Lindenfors & Tullberg, 1998; Lindenfors, 2002a) and is a common pattern in many other animals (Abouheif & Fairbairn, 1997). In this study we find that male wing length has increased more than female wing length over evolutionary time after transitions towards more socially polygynous mating systems. In addition, in none of the alternative reconstructions, neither for body mass nor wing length, did female body size change more than male body size. The opposite relationship was, however, significant in many cases.

The combined results suggest the scenario in Fig. 6, which shows body size evolution of each sex separately according to the impacts of sexual selection in different mating systems. This encompasses three of our key observations: (1) greater variability in body size of males than of females, (2) transitions towards more polygyny accompanied by increased male-biased dimorphism as well as increased male and female body size, and, (3) transitions towards more polyandry associated with increased female-biased dimorphism and reduced male and female body size. The only way for these significant results to be true at the same time without contradicting



**Fig. 6** A schematic explanation for how male- and female-biased sexual size dimorphism evolve as a result of sexual selection on males and females.

each other is, first, if male body size increases more than female body size after transitions towards a more polygynous mating system (as predicted by sexual selection theory) and secondly, if male body size decreases more than female body size after transitions towards a more polyandrous mating system (Fig. 6).

We were surprised to find that transitions towards social polyandry have entailed female size decreases rather than increases, given the pronounced reversal in courtship roles that accompany these transitions in many shorebirds. For example, in spotted sandpipers (*Tringa macularia*) and most species of jacanas (*Jacana* spp.), females fight conspicuously for mates and territories, and they are markedly larger than males (Oring, 1986; Emlen *et al.*, 1989; Butchart *et al.*, 1999). However, the jacanas represent just one evolutionary transition towards role-reversal, and spotted sandpipers yield one more, thus contributing two data points to the overall analyses of such transitions. Size dimorphism is much lower in role-reversed phalaropes (*Phalaropus* spp.) and dotterel (*Charadrius morinellus*) (Reynolds, 1987).

We can speculate on possible reasons for females not becoming larger after transitions to social polyandry. In some role-reversed species, female mating success may depend less on size-related advantages in competitive interactions than does the success of males in species that have conventional sex roles. Instead, there may be constraints on female size due to the demands of producing multiple clutches. But why has male size decreased more than female size after transitions towards a more polyandrous mating system? One possibility is

that females might prefer smaller males, as in the case of moorhens (*Gallinula chloropus*), a species in which males contribute towards incubation (Petrie, 1983). If this occurs in shorebirds too, this could select for smaller male size.

Perhaps display agility (Figuerola, 1999; Székely *et al.*, 2000) is the crucial variable that can explain this pattern, although we could not validate this hypothesis in the current study. It is hard to see, however, why display agility should be more important in socially polyandrous species than in nonpolyandrous ones. In fact, to the best of our knowledge there are no socially polyandrous species in which males use agile display flights other than a twisting flight that male phalaropes use to chase away unwanted suitors (Reynolds, 1987). Although the same data set as used here has previously been utilized in analyses to support the influence of display type (Székely *et al.*, 2000), these results could not be replicated with the directional analyses used here. Further analyses, perhaps on a larger data set, are needed to resolve this issue.

For the present study, we would like to offer the following scenario, which fits with the observations in this study, although we are not, by any means, convinced that it is correct! Suppose the optimal size (without sexual selection) for both sexes is  $x$ . Sexual selection on males forces males to become  $x + 3$ . Females get dragged along by genetic correlation to become  $x + 2$ . In role-reversed species males are able to revert to size  $x$  because there is very little sexual selection acting on them. Females now get dragged by males the other way, stopping at  $x + 1$ . Females do not go all the way to  $x$  because sexual selection is acting on them to compete for males. One might think of this as a male chauvinistic rubber band hypothesis. It is chauvinistic because it focuses on selection acting on males, and the rubber band is the genetic correlation that drags females either up or down in size according to selection on males. Our scepticism about this idea is fuelled by the fact that in socially polyandrous species, females clearly are under strong sexual selection, including aggressive behaviour that must surely exert pressures for large size. To refute the hypothesis, we need to be able to compare the magnitude of such selection pressures on both sexes, and the degree to which they are opposed by natural selection pressures, such as those involving fecundity and parental care.

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