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SEXUAL SIZE DIMORPHISM IN SHOREBIRDS, GULLS, AND ALCIDS: THE INFLUENCE OF SEXUAL AND NATURAL SELECTION

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Abstract.—Charadrii (shorebirds, gulls, and alcids) have an unusual diversity in their sexual size dimorphism, ranging from monomorphism to either male-biased or female-biased dimorphism. We use comparative analyses to investigate whether this variation relates to sexual selection through competition for mates or natural selection through different use of resources by males and females. As predicted by sexual selection theory, we found that in taxa with socially polygynous mating systems, males were relatively larger than females compared with less polygynous species. Furthermore, evolution toward socially polyandrous mating systems was correlated with decreases in relative male size. These patterns depend on the kinds of courtship displays performed by males. In taxa with acrobatic flight displays, males are relatively smaller than in taxa in which courtship involves simple flights or displays from the ground. This result remains significant when the relationship with mating system is controlled statistically, thereby explaining the enigma of why males are often smaller than females in socially monogamous species. We did not find evidence that evolutionary changes in sexual dimorphism relate to niche division on the breeding grounds. In particular, biparental species did not have greater dimorphism in bill lengths than uniparental species, contrary to the hypothesis that selection for ecological divergence on the breeding grounds has been important as a general explanation for patterns of bill dimorphism. Taken together, these results strongly suggest that sexual selection has had a major influence on sexual size dimorphism in Charadrii, whereas divergence in the use of feeding resources while breeding was not supported by our analyses.

Key words.—Charadrii, display behavior, niche division, sexual selection, size dimorphism, waders.

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Differences between males and females in body size are striking in many animals. Several hypotheses have been advanced to explain sexual size dimorphism (reviewed by Hedrick and Temeles 1989; Shine 1989; Mueller 1990; Andersson 1994). Sexual selection was proposed originally by Darwin (1871). In particular, if competition between members of one sex (typically males) is more intense than between members of the other sex, then sexual selection is expected to lead to larger size in the more competitive sex. The selective advantage of body size, however, may depend on whether the competition occurs on the ground or in the air (Payne 1984; Jehl and Murray 1986; Höglund 1989). In particular, if males fight on the ground, then large size may be selectively advantageous, whereas if competition occurs in the air, then small males may benefit from enhanced maneuverability (Andersson and Norberg 1981). This may help males compete for territories, and females may prefer the most acrobatic males (Hedenström and Møller 1992; Grønstøl 1996; Hakkarainen et al. 1996).

Natural selection due to ecological differences between the sexes is an alternative to sexual selection as a cause of sexual dimorphism (Shine 1989; Andersson 1994). This could occur in several ways. First, if both parents remain in the vicinity of the young, there could be selection for divergent ecological specialisation through advantages of reduced competition between members of the pair if food is limiting (Selander 1972; Shine 1989). Males and females often do exploit different resources (e.g., Temeles and Roberts 1993; Pierre 1994; Aho et al. 1997), but this cannot be taken as evidence in favor of the intrapair competition hypothesis because cause and effect are unclear. Note too that this hypothesis does not specify the direction of dimorphism between the sexes; either males or females may be the smaller sex. The second way in which natural selection could explain sexual dimorphism is if one sex (e.g., females) gains more in fecundity per unit body size than the other sex gains through mating advantages (reviewed in Andersson 1994). This is apt to be particularly true when the female's body cavity limits egg production (e.g., in many fishes and frogs) and when males invest more into searching for and displaying to females than fighting for them. Third, if only one parent provides care for the offspring, natural selection to perform efficient care could influence its body size. For example, large animals may be better at defending nests from predators. In the case of raptors, where females are more active in nest defense, this is one potential explanation for females being larger than males (Mueller 1990). Alternatively, small body size may be favored in the incubating parent if this aids energetic efficiency (Jönsson and Alerstam 1990).

The suborder Charadrii (shorebirds, gulls, and alcids, 365 species) is an excellent group to investigate hypotheses about sexual size dimorphism because these birds show extreme variation in dimorphism, encompassing nearly the entire range found in birds (Jehl and Murray 1986). Furthermore, among shorebirds, gulls, and alcids, there is unusually high variation in sexual selection and parental care, including social monogamy, polygyny, and polyandry and biparental care, male-only care, and female-only care (Erckmann 1983; Székely and Reynolds 1995). The development of young is also variable; in most sandpipers and allies the chicks are precocial, whereas in gulls and alcids the parents provision their chicks for a substantial period of time. Thus, both the range of dimorphism and of traits correlated with alternative hypotheses to explain it are broad enough to test for general explanations.

The objective of this study is to investigate the significance of both sexual and natural selection in the evolution of sexual size dimorphism in Charadrii. Sexual selection theory predicts that the relative size of the more competitive sex should increase with increasing competition for mates. The effect of sexual selection is expected to be moderated by the type of courtship display (Jehl and Murray 1986). We therefore tested the prediction that in species in which males perform acrobatic displays, the relative size of males should be less than in species where males are less acrobatic. To investigate the influence of natural selection through ecological specialization on the breeding grounds, we test the prediction that bill length should be more sexually dimorphic in biparental species than in uniparental ones. This could be due to selection to avoid competition between male and female parents for food or differences in ecological efficiency irrespective of intrapair competition.

MATERIALS AND METHODS

Data and Phylogeny

Morphometric data (body mass, wing length, bill length) and behavioral data (mating system, display type, parental care) were collected from the literature (Appendix 1). Social mating system was scored as polygynous (1), monogamous (2), or polyandrous (3). These scores were based on statements concerning mating system in primary sources or in reference books (Cramp and Simmons 1983; Cramp 1985; Marchant and Higgins 1993; Higgins and Davies 1996; del Hoyo et al. 1996, 1997; see Appendix 1). Display type of males was scored as ground display (1); aerial nonacrobatic display (2); or aerial acrobatic display (3). These scores were based upon Jehl and Murray (1986, table IV) and the sources given in Appendix 1. A display was considered to be acrobatic if it includes steep dives and climbs, twists, and turns. Our display scores agreed with the scores of an observer who was unaware of the objective of the study (nine of nine species). The duration of care was scored separately for males and females as 0–7 (see Székely and Reynolds 1995): if a sex neither incubates nor attends the young it was scored 0 and if it attends the brood until the chicks fledge it was scored 7.

The phylogeny initially was based on Reynolds and Székely (1997; see the rationale in Székely and Reynolds 1995). We expanded this phylogenetic framework by adding *Attagis, Himantopus, Recurvirostra, Burhinus, Chionis,* and Laroidea (pratincoles, gulls, and alcids, Fig. 1). The phylogenetic positions of these genera are given by Sibley and Ahlquist (1990, figs. 363–365). Borowik and McLennan (1999) have recently proposed two new phylogenetic hypotheses for calidrine sandpipers, based on molecular evidence. We understand that work is continuing in this clade, but we have adopted their provisional hypotheses and used them to replace Baker's (1992) earlier calidrine phylogeny, which had been used by Reynolds and Székely (1997). In fact, we repeated all analyses using the original calidrine phylogeny embedded in the tree shown here, and found no differences in the results (not shown). Furthermore, although we provide only the results from the maximum-likelihood phylogeny of Borowik and McLennan (1999), tests with their maximum-parsimony tree also produced consistent results with the ones shown. Thus, although the phylogeny is still in a state of flux, our results are robust for the phylogenetic hypotheses that have been published to date.

In some clades the mating system and display type were highly conservative. For example, in stone-curlews, oystercatchers, terns, and alcids both the social mating system and display type are invariable (Cramp and Simmons 1983; Cramp 1985; del Hoyo et al. 1996; Higgins and Davies 1996). From these genera we chose a single representative for which the most information was available; adding more species would not yield more comparisons for these analyses. Several species from a genus were included if they had different mating behaviors or display types (e.g., *Scopolax, Coenocorypha, Gallinago, Calidris, Larus*).

To reduce sampling errors in morphometric measurements, we included only those species for which at least five males and females each were measured, except for *Calidris ptilocnemis, Gallinago media,* and *Thinocorus rumicivorus,* for which the sample sizes were not provided in the original sources. If several sets of data were available for a species, we used the ones that were taken during the breeding season or that were based on the largest sample. Taxon names are used as given by Monroe and Sibley (1993).

Phylogenetic Analyses

Comparative analyses of mating system and display type were carried out in two ways. First, we used Felsenstein's (1985) method and evaluated phylogenetically independent contrasts (''contrasts,'' hereafter) in morphology, mating system, and display type as implemented by Purvis and Rambaut (1995). This method incorporates phylogenetic relationships into statistical analyses to ensure that the degrees of freedom are not inflated by nonindependent samples (Harvey and Pagel 1991). Body mass, wing length, and bill length were log transformed (base 10). We considered mating system and display type as categorical variables, and we split them into two dummy variables each (Zar 1996). In case of mating system, these variables allowed us to calculate the transitions between taxa toward either a greater amount of polygyny or toward a greater amount of polyandry. In case of display type, the dummy variables allowed us to calculate the transitions between taxa toward either ground display or toward acrobatic displays. The dummy variables were analysed using the Crunch option of CAIC (Purvis and Rambaut 1995; see also Møller and Birkhead 1993; Martin and Clobert 1996; Badyaev 1997). This approach involves comparisons between all nodes in the tree and, as such, makes more assumptions than when comparisons are restricted to terminal taxa (see also Harcourt et al. 1995). We therefore repeated our analyses restricting the comparisons to terminal taxa, that is, without comparing internal nodes (see below). Branch lengths were set to unity (Purvis and Rambaut 1995) because branch

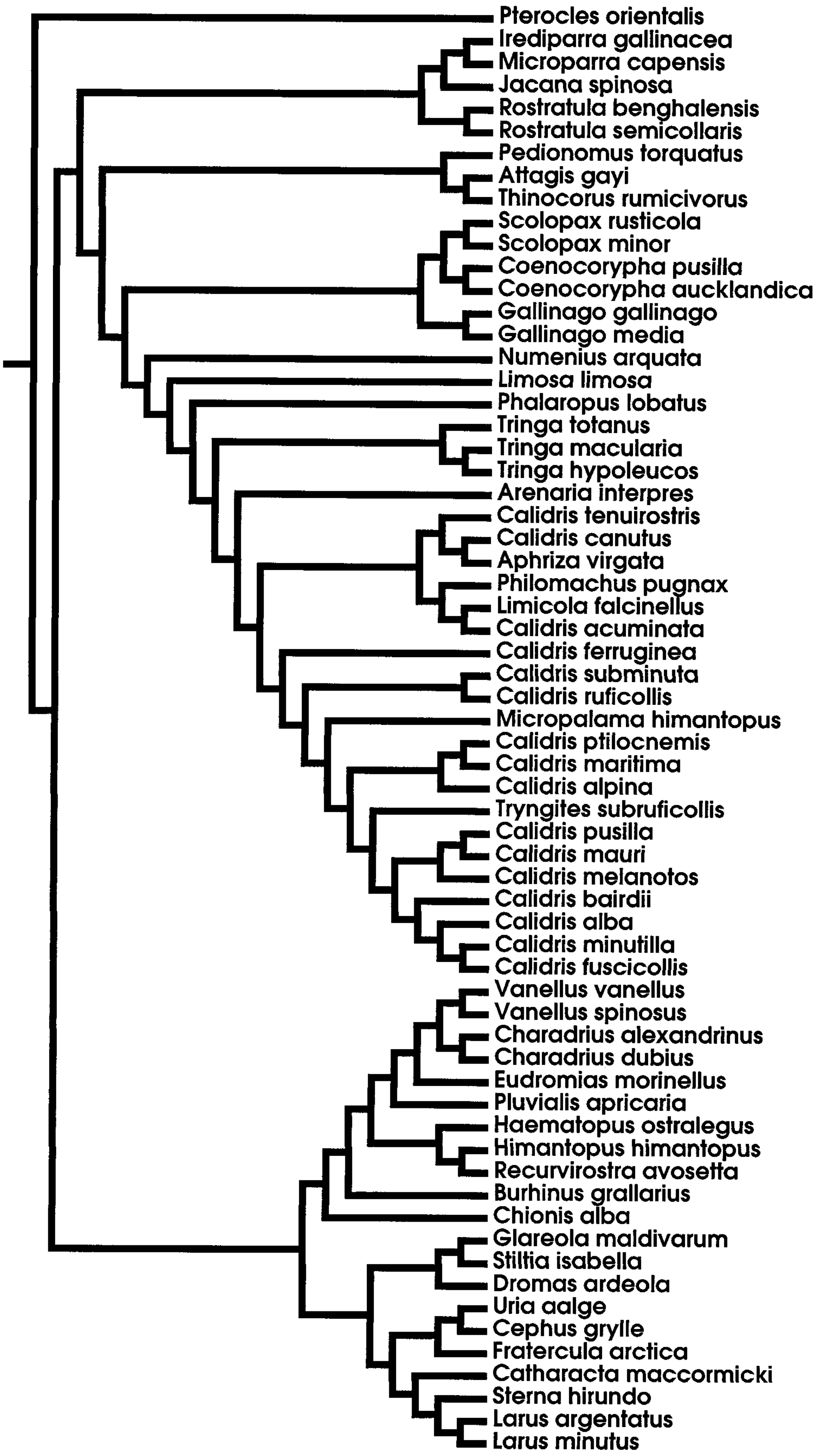

FIG. 1. Phylogeny of Charadrii (see Materials and Methods for justification).

lengths between many nodes were not known. An assumption of Felsenstein's (1995) method is that the absolute values of the contrasts are independent of their standard deviations (Garland et al. 1992; Purvis and Rambaut 1995). This assumption was met by all continuous variables.

Univariate and multivariate regressions between contrasts were forced through zero (Harvey and Pagel 1991; Garland et al. 1992), and we report *r*, the correlation coefficient, and $F_{\text{df regression,df error}}$. Evolutionary differences (i.e., contrasts) in size were highly correlated between males (dependent variables) and females (body mass: $r = 0.983$, $F_{1,56} = 1619.252$, $P < 0.0001$; wing length: $r = 0.985$, $F_{1,62} = 2030.772$, $P < 0.0001$). The residuals of these regressions were used as the measures of sexual size dimorphism. The dummy variables representing either the mating system or the display type were entered in one step into the models and we provide the statistics for each.

We also investigated the relationships between dimorphism, mating system and display type by controlling for the effects of either mating system or display type in multiple regressions. In the latter analyses the change in r^2 (r^2_{change}) and the value of F (F_{change}) due to either the mating system or the display were calculated as given by Norušis (1988). All multivariate models of mating system and display type were repeated by excluding contrasts that had zero values in both dummy variables to improve homoscedascity. The exclusion of these contrasts does not change our conclusions (results not shown).

We also analyzed the relationships between sexual size dimorphism, mating system, and display type by paired tests (Briskie et al. 1994; Harvey and Nee 1997), that is, without reconstructing internal nodes. Residual male mass and wing length were calculated by regressing male measurements onto female measurements using only the species given in Appendix 2. For the analyses of mating system, we chose species pairs in which female-female competition in one species was expected to be more intense (i.e., the species was more socially polyandrous) than in the other in which the intensity of male-male competition was expected to be more intense (i.e., more polygynous). Examples of species pairs that conformed to this criterion were polyandrous-monogamous, polyandrous-polygynous, and monogamous-polygynous (Appendix 2a). If several species were available for a pair, then the mean of the species were included. For the analyses of display type we chose species pairs in which the display behavior was different (Appendix 2b). Because mating system was related to dimorphism (see Results), we controlled for mating systems by choosing pairs in which both members of the pair had a similar social mating system (e.g., both monogamous or polygynous). If several species were available for the analyses, we used their means in the analyses.

The niche-division hypothesis was analysed by using dimorphism in bill length and the duration of parental care in two ways. First, we performed separate analyses on each sex to obtain phylogenetically independent contrasts in bill length. Then we regressed the contrasts in male bill length onto contrasts in female bill length ($r = 0.988$, $F_{1,60} = 2410.370$, $P < 0.0001$) and we retained the residuals of the regression (bill dimorphism). The absolute value of these contrasts indicates the extent of change in dimorphism (absolute bill dimorphism), because a large residual value in either a negative or positive direction indicates a large evolutionary difference. Next, we regressed contrasts in the duration of male care onto contrasts in the duration of female care ($r = -0.431$, $F_{1,60} = 13.700$, $P = 0.0005$). Scores of care duration had been arcsine transformed, that is, we took the arcsine of the square root of the score of duration of care divided by the score of maximum duration of care (score = 7). We used residuals from this regression (residual care). Positive residuals indicate relatively more biparental care for a given level of female care and negative residuals indicate the opposite. Finally, the absolute bill dimorphism calculated above was regressed onto residual care and we report the statistics of this regression. Absolute bill dimorphism was analyzed by a nonzero intercept model of linear regression because the direction of subtraction between two nodes was no longer arbitrary (as in standard analyses of contrasts; Garland et al. 1992); rather, all contrasts were made positive.

The second way of analyzing niche division involved paired comparisons whereby higher nodes were not reconstructed. Instead, species pairs were selected in which one member of the pair had a longer period of biparental care than the other (Appendix 2c). If several species were available for the analyses (i.e., having an identical duration of biparental care) we took their means. Male bill length was regressed onto female bill length and the residuals were taken. We made the residuals positive and compared them using paired tests between more biparental and less biparental species. All variants of the niche-division hypothesis predict that larger residuals should be observed in the more biparental species than in the less biparental one. In addition, because mating system is related to dimorphism (see Results), we also selected species pairs in which the mating system of both members of the pair was similar and repeated the preceding analysis with this reduced data set (Appendix 2d).

Mean ± SE as well as the probabilities of two-tailed tests are given throughout the paper. Nonparametric tests were used if the standard assumptions of parametric tests were not met.

RESULTS

Correlations among Forms of Dimorphism

Differences in dimorphism of body mass, wing length, and bill length were highly correlated as follows: mass dimorphism (dependent variable) and wing dimorphism: $r = 0.848$, $F_{1,56} = 143.602$, $P < 0.0001$; mass dimorphism and bill dimorphism: $r = 0.756$, $F_{1,56} = 74.590$, $P < 0.0001$; wing dimorphism and bill dimorphism: $r = 0.675$, $F_{1,62} = 51.777$, $P < 0.0001$.

Mating System

Evolutionary differences in mating system were related to changes in dimorphism in the manner predicted by sexual selection (Table 1; mass: $r^2 = 0.139$, $F_{2,55} = 4.426$, $P = 0.017$; wing length: $r^2 = 0.299$, $F_{2,60} = 12.779$, $P < 0.0001$). In particular, the partial correlation coefficients in Table 1 show that changes toward a more polygynous mating system corresponded with increases in mass and wing length of males

TABLE 1. Partial correlation coefficients (*r*) between phylogenetic contrasts in sexual size dimorphism (dependent variable, male vs. female) and mating system and display type (independent variables). Mating system and display type are represented by two dummy variables each (see Materials and Methods for details). *F*- and *P*-values are provided for the four models as well as for each dummy variable.

	Dimorphism in body mass			Dimorphism in wing length		
	r	*F*	*P*	*r*	*F*	*P*
Mating system[1]		4.426	0.017		12.779	<0.0001
Toward polygyny	0.308	6.290	0.015	0.370	12.517	0.0008
Toward polyandry	−0.177	2.036	0.159	−0.362	11.717	0.001
Display type[2]		10.840	0.0001		12.808	<0.0001
Toward ground display	0.074	0.342	0.561	−0.041	0.115	0.736
Toward acrobatic display	−0.495	15.579	0.0002	−0.570	22.165	<0.0001

[1] The degrees of freedom (regression, error) of the models are 2, 55 (body mass) and 2, 60 (wing length).

[2] The degrees of freedom of the models are 2, 54 (body mass) and 2, 58 (wing length).

relative to females, whereas evolutionary differences toward a more polyandrous mating system corresponded with reductions in wing length of males relative to females, although the mass relationship was not significant (Table 1). These results were confirmed by paired tests (Appendix 2a), because males were relatively smaller in more polyandrous species than in more polygynous ones (Fig. 2; Wilcoxon matched-pairs tests, mass dimorphism: $z = 2.291$, $n = 14$, $P = 0.022$; wing dimorphism: $z = 2.627$, $n = 17$, $P = 0.009$).

These changes in dimorphism may be caused by sexual selection acting either on males or on females. To investigate these possibilities, we excluded either the socially polyandrous or polygynous species from the analyses. In both cases the relationships remained highly significant between mating system and dimorphism: with polyandrous species excluded, for mass dimorphism: $r^2 = 0.130$, $F_{1,48} = 7.158$, $P = 0.010$; for wing dimorphism: $r^2 = 0.192$, $F_{1,53} = 12.564$, $P = 0.0008$; with polygynous species excluded, for mass dimorphism: $r^2 = 0.139$, $F_{1,45} = 7.238$, $P = 0.010$, and for wing dimorphism $r^2 = 0.506$, $F_{1,50} = 51.227$, $P < 0.0001$.

Display Type

Evolutionary differences in display behavior were associated with changes in male:female body mass and wing length (Table 1; mass dimorphism: $r^2 = 0.287$, $F_{2,54} = 10.840$, $P = 0.0001$; wing dimorphism: $r^2 = 0.306$, $F_{2,58} = 12.808$, $P < 0.0001$). In particular, changes toward acrobatic displays corresponded with decreases in mass and wing length of males relative to females (Table 1). These results were confirmed by paired tests (Appendix 2b, Fig. 3): In more acrobatic taxa, males were smaller (relative to females) than in less acrobatic taxa (Wilcoxon matched-pairs tests, mass dimorphism: $z = 2.497$, $n = 10$, $P = 0.0125$; wing dimorphism: $z = 2.589$, $n = 12$, $P = 0.0096$).

We also investigated whether the reductions in male:female dimorphism were related specifically to acrobatic displays. When taxa exhibiting acrobatic displays are excluded and comparisons restricted to species exhibiting ground versus nonacrobatic aerial displays, the relationship is no longer significant between dimorphism and display behavior (mass dimorphism: $r^2 = 0.002$, $F_{1,28} = 0.049$, $P = 0.826$; wing dimorphism: $r^2 = 0.003$, $F_{1,31} = 0.028$, $P = 0.867$). In contrast, exclusion of ground displaying species does not change the relationship (mass dimorphism: $r^2 = 0.315$, $F_{1,40} = 18.348$, $P = 0.0001$; wing dimorphism: $r^2 = 0.415$, $F_{1,41} = 29.120$, $P < 0.0001$). These results match the partial correlation coefficients in Table 1, suggesting that the reduction in relative male size is not just related to the evolution of aerial displays, but of acrobatic displays in particular.

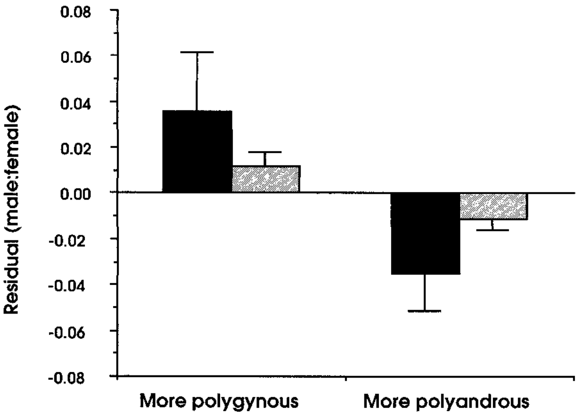

FIG. 2. Paired comparisons of sexual dimorphism between more polygynous and more polyandrous species. Means ± SEs of residuals from regressions of male contrasts versus female contrasts are shown for body mass (black, $n = 14$) and wing length (gray, $n = 17$).

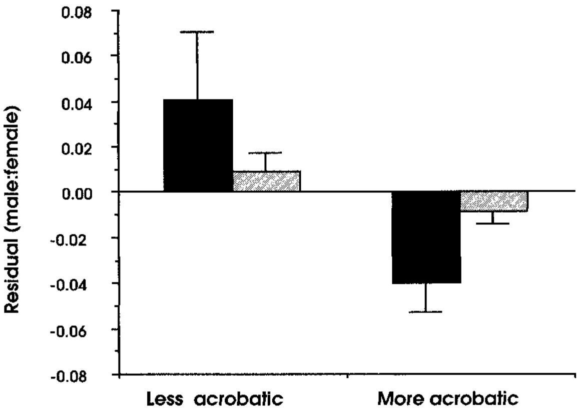

FIG. 3. Paired comparisons of sexual dimorphism between taxa where males are more or less acrobatic. Means ± SEs of residuals from regressions of male contrasts versus female contrasts are shown for body mass (black, $n = 10$) and wing length (gray, $n = 12$).

Finally, we investigated the relationships between evolutionary differences in display type and dimorphism by statistically controlling for mating system (full models that included both mating system and display type: mass dimorphism: $r^2 = 0.439$, $F_{4,52} = 10.172$, $P < 0.0001$; wing dimorphism: $r^2 = 0.575$, $F_{4,55} = 18.634$, $P < 0.0001$). These models showed that the relationship between evolutionary differences in dimorphism and display type remain significant once mating system is controlled for (mass dimorphism: $r^2_{\text{change}} = 0.300$, $F_{\text{change}2,51} = 13.623$, $P < 0.001$, wing dimorphism: $r^2_{\text{change}} = 0.306$, $F_{\text{change}2,54} = 19.471$, $P < 0.001$). Furthermore, the relationship between evolutionary differences in dimorphism and mating system remains significant once display type is controlled for (mass dimorphism: $r^2_{\text{change}} = 0.153$, $F_{\text{change}2,51} = 6.932$, $P < 0.005$, wing dimorphism: $r^2_{\text{change}} = 0.266$, $F_{\text{change}2,54} = 16.902$, $P < 0.001$).

Niche Division

Relationships between biparental care and bill dimorphism were investigated by three analyses, none of which supported the hypothesis that selection for niche division on the breeding grounds has influenced overall patterns of sexual dimorphism in bill length. First, differences among taxa in absolute bill dimorphism were not related to evolutionary differences in residual parental care (absolute bill dimorphism = 0.0102 − [0.0010 × residual care], $r^2 = 0.003$, $F_{1,59} = 0.165$, $P = 0.687$). Second, in paired tests (Appendix 2c), bill dimorphism did not differ between more biparental species (mean = 0.0183 ± 0.0017) and less biparental ones (0.0255 ± 0.0047; Wilcoxon matched-pairs test, $z = 1.167$, $n = 19$, $P = 0.243$). Third, we repeated the preceding analysis using species pairs in which the mating system of the species pairs was similar (Appendix 2d). Bill dimorphism remained nonsignificantly different between these species pairs (more biparental species: mean = 0.0201 ± 0.0026, less biparental species: 0.0187 ± 0.0040, Wilcoxon matched-pairs test, $z = 0.445$, $n = 11$, $P = 0.657$).

DISCUSSION

Our results are consistent with the hypothesis that sexual size dimorphism has evolved in Charadrii due to sexual selection. In particular, mating system was an important predictor of dimorphism, with increases in the intensity of male-male competition matching increases in body mass and wing length of males relative to females and vice versa for increases in female competition, although the trend was not significant for mass. The relationship with female-female competition contrasts with the conclusion of Mueller (1990), which was based mainly on raptors, that competition for males does not select for large size in females. Our results are consistent between two kinds of phylogenetic analyses and three phylogenetic hypotheses.

Our results are also consistent with the hypothesis that acrobatic displays select for small size in males (Andersson and Norberg 1981; Payne 1984; Jehl and Murray 1986). This finding matches single-species studies in shorebirds and raptors, which indicate that small size is advantageous in performance of acrobatic aerial displays (Blomqvist et al. 1997) and that performance of such displays correlates with mating success (Grønstøl 1996; Hakkarainen et al. 1996). Our results thus provide the first quantitative support in a phylogenetic framework for Jehl and Murray's (1986) hypothesis that sexual size dimorphism is linked to aerial displays in shorebirds. Our findings also support the study by Figuerola (1999) of monogamous shorebirds. He found that males were smaller in acrobatic species than in nonacrobatic ones. Our results extend these previous studies by showing (1) it is not simply the presence or absence of aerial displays that matters, but specifically the presence of acrobatic displays that matches reduced male size relative to females; (2) the pattern remains significant when the effects of mating systems are controlled statistically; and (3) the results hold for Charadrii in general.

None of our analyses support the niche division hypothesis. Thus, selection for different niche utilization between males and females on the breeding grounds does not explain the observed variation in dimorphism in Charadrii. There may be several reasons for this. First, in many biparental shorebirds and gulls only one parent attends the chicks at a time, whereas the other one feeds away from the territory. This would reduce selection for different aspects of morphology such as bill lengths of males and females. Second, resources may be abundant or vary in space or time, again resulting in low selection for different feeding methods and morphologies associated with them. Third, competition with other individuals in the population as well as with other species throughout the year may be more important than competition within a pair during the breeding season. Thus, although there may be selection and adaptations for males and females to utilize different resources in some Charadrii, we conclude that niche utilization on the breeding grounds does not provide a general explanation for the patterns of size dimorphism in this clade.

Other hypotheses of size dimorphism, which focus on the fact that selection should act on each sex separately (Reynolds and Harvey 1994), remain to be tested. Thus, although the patterns shown here support a role for sexual selection, they could be driven by changes in morphology of either or both sexes, which would need to be analyzed in conjunction with additional variables not included here. For example, female size may be selected to increase fecundity or egg size (Selander 1972). Several studies have shown that larger female shorebirds lay larger eggs (e.g., Sandercock 1998). However, Olsen and Cockburn (1993) and Weatherhead and Teather (1994) analyzed the patterns of size dimorphism and body and egg mass in waders and other birds and did not find evidence to support this hypothesis, although their analyses did not incorporate phylogenetic relatedness. It has also been suggested that dimorphism in feeding apparatus such as in bill morphology may have evolved through adaptation by each sex to exploit different resources (Jönsson and Alerstam 1990). For example, in dunlin *Calidris alpina*, the male stays with the chicks in a terrestrial habitat, while the female deserts her brood and feeds on mudflats. Thus, the size of the male's bill may be adapted to exploit terrestrial food, whereas female bills are better suited for probing in mud. Our finding that bill dimorphism was not greater in less biparental species does not support this hypothesis as a general explanation, although if sufficient data were available, it would be better to compare bill dimorphism directly with feeding habits of male and female birds.

Our study has focused on selective forces that may operate during the breeding season. Nevertheless, shorebirds, gulls, and alcids spend considerable amounts of time, often up to 10 months, away from their breeding areas. Thus, the ecological conditions they face during migration and winter may differ substantially between the breeding and the nonbreeding seasons. For example, males and females may use different sites or habitats during migration and winter (Ketterson and Nolan 1983). Future comparative analyses are required to test how natural selection to exploit the resources over the nonbreeding season may have shaped dimorphism in Charadrii. For instance, future studies may investigate whether different migratory and wintering strategies select for a particular morphological difference between the sexes.

In conclusion, our study supports a role for sexual selection in the evolution of sexual size dimorphism in Charadrii, and specifically the importance of acrobatic aerial displays causing males to evolve a smaller size than females. There is a limit to how far one can disentangle effects of sexual and natural selection, because sex differences in habitat use and migration are apt to be an outcome of the interplay between sexual selection and parental care (Reynolds and Székely 1997). Nevertheless, patterns of bill dimorphism do not support the hypothesis that selection for niche division through intrapair competition while breeding has been important, although we cannot rule out a role for other aspects of ecological specialization during the nonbreeding season.

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LITERATURE CITED

Aho, T., M. Kuitunen, J. Suhonen, T. Hakkari, and A. Jäntti. 1997. Effects of male removal on female foraging behavior in the Eurasian treecreeper. Behav. Ecol. Sociobiol. 41:49–53.

Andersson, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.

Andersson, M., and R. A. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biol. J. Linn. Soc. 15:105–130.

Badyaev, A. B. 1997. Covariation between life history and sexually selected traits: an example with cardueline finches. Oikos 80: 128–138.

Baker, A. J. 1992. Molecular genetics of *Calidris*, with special reference to knots. Wader Study Group Bulletin 64:S29–S35.

Blake, E. R. 1977. Manual of Neotropical birds. Vol. 1. Univ. of Chicago Press, Chicago, IL.

Blomqvist, D., O. C. Johansson, U. Unger, M. Larsson, and L.-A. Flodin. 1997. Male aerial display and reversed sexual size dimorphism in the dunlin. Anim. Behav. 54:1291–1299.

Borowik, O. A., and D. A. McLennan. 1999. Phylogenetic patterns of parental care in Calidrine sandpipers. Auk 116:1107–1117.

Briskie, J. V., C. T. Naugler, and S. M. Leech. 1994. Begging intensity of nestling birds varies with sibling relatedness. Proc. Roy. Soc. London B. 258:73–78.

Byrkjedal, I., G. B. Grønstøl, T. P. Lislevand, M. Kjell, H. Sandvik, and S. Stalheim. 1997. Mating systems and territory in lapwings *Vanellus vanellus*. Ibis 139:129–137.

Colston, P., and P. Burton. 1988. A field guide to the waders of Britain and Europe with North Africa and the Middle East. Hodder and Stoughton, London.

Cramp, S. 1985. The birds of the Western Palearctic. Vol. 4. Oxford Univ. Press, Oxford, U.K.

Cramp, S., and K. E. L. Simmons. 1983. The birds of the Western Palearctic. Vol. 3. Oxford Univ. Press, Oxford, UK.

Darwin, C. 1871. The descent of man and selection in relation to sex. Murray, London.

del Hoyo, J., A. Elliott, and J. Sargatal, eds. 1996. Handbook of the birds of the world. Vol. 3. Lynx Edicions, Barcelona, Spain.

———. 1997. Handbook of the birds of the world. Vol. 4. Lynx Edicions, Barcelona, Spain.

Dunning, J. B., Jr. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, FL.

Erckmann, W. J. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. Pp 113–168 *in* S. K. Wasser, ed. Social behavior of female vertebrates. Academic Press, New York.

Felsenstein, J. 1985. Phylogenies and the comparative method. Am. Nat. 125:1–15.

Figuerola, J. 1999. A comparative study on the evolution of reversed size dimorphism in monogamous waders. Biol. J. Linn. Soc. 67: 1–18.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst. Biol. 41:18–32.

Grønstøl, G. B. 1996. Aerobatic components in the song-flight display of male lapwings *Vanellus vanellus* as cues in female choice. Ardea 84:45–55.

Hakkarainen, H., E. Huhta, K. Lahti, P. Lundvall, T. Mappes, P. Tolonen, and J. Wiehn. 1996. A test of male mating and hunting success in the kestrel: the advantages of smallness? Behav. Ecol. Sociobiol. 39:375–380.

Harcourt, A. H., A. Purvis, and L. Liles. 1995. Sperm competition: mating system, not breeding season, affects testes size of primates. Funct. Ecol. 9:468–476.

Harvey, P. H., and S. Nee. 1997. The phylogenetic foundations of behavioural ecology. Pp 334–349 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Blackwell, Oxford, U.K.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford Univ. Press, Oxford, U.K.

Hedenström, A., and A. P. Møller. 1992. Morphological adaptations to song flight in passerine birds: a comparative study. Proc. R. Soc. Lond. B 247:183–187.

Hedrick, A. V., and E. J. Temeles. 1989. The evolution of sexual dimorphism in animals: hypotheses and test. Trends Ecol. Evol. 4:136–138.

Higgins, P. J., and S. J. J. F. Davies. 1996. Handbook of Australian, New Zealand, and Antarctic birds. Vol. 3. Oxford Univ. Press, Oxford, U.K.

Höglund, J. 1989. Size and plumage dimorphism in lek-breeding birds: a comparative analysis. Am. Nat. 134:72–87.

Jehl, J. R., Jr. 1973. Breeding biology and systematic relationships of the stilt sandpiper. Wilson Bull. 85:115–147.

Jehl, J. R., Jr., and B. G. Murray, Jr. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. Pp. 1–86. *in* R. F. Johnston, ed. Current ornithology. Vol. 3. Plenum Press, New York.

Jenni, D. A., and G. Collier. 1972. Polyandry in the American jacana (*Jacana spinosa*). Auk 89:743–765.

Johnsgard, P. A. 1981. The plovers, sandpipers, and snipes of the World. Univ. of Nebraska Press, Lincoln, NE.

Jönsson, P. E., and T. Alerstam. 1990. The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. Biol. J. Linn. Soc. 41:301–314.

Ketterson, E. D., and V. Nolan, Jr. 1983. The evolution of differential bird migration. Pp. 357–402 *in* Johnston, R. F., ed. Current ornithology. Vol. 1. Plenum Press, New York.

MacLean, G. L. 1969. A study of seedsnipe in southern South America. Living Bird 8:33–80.

Marchant, S., and P. J. Higgins. 1993. Handbook of Australian, New Zealand, and Antarctic birds. Vol. 2. Oxford Univ. Press, Oxford, U.K.

Martin, T. E., and J. Clobert. 1996. Nest predation and avian life-history evolution in Europe versus North America: a possible role of humans? Am. Nat. 147:1028–1046.

Monroe, B. L., and C. G. Sibley. 1993. A world checklist of birds. Yale University Press, New Haven, CT.

Møller, A. P., and T. R. Birkhead. 1993. Cuckoldry and sociality: a comparative study of birds. Am. Nat. 142:118–140.

Mueller, H. C. 1990. The evolution of reversed sexual dimorphism in size in monogamous species of birds. Biol. Rev. 65:553–585.

Myers, J. P., O. Hildén, and P. S. Tomkovich. 1982. Exotic *Calidris* species of the Siberian tundra. Ornis Fennica 59:175–182.

Norušis, M. J. 1988. SPSS-X advanced statistics guide. SPPS Inc., Chicago, IL.

Oliver, W. R. B. 1955. New Zealand birds. Reed, Wellington, New Zealand.

Olsen, P. D., and A. Cockburn. 1993. Do large females lay small eggs? Sexual dimorphism and the allometry of egg and clutch volume. Oikos 66:447–453.

Payne, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. Ornithol. Monogr. 33:1–53.

Pierre, J. P. 1994. Effects of sexual dimorphism on feeding behaviour of the bar-tailed godwit (*Limosa lapponica*) at a southern hemisphere wintering site. New Zealand Nat. Sci. 21:109–112.

Pitelka, F. A., R. T. Holmes, and S. F. MacLean, Jr. 1974. Ecology and evolution of social organization in arctic sandpipers. Am. Zool. 14:185–204.

Poole, A. F., and F. B. Gill, eds. 1992. The birds of North America. The Academy of Natural Sciences, Philadelphia, PA.

Prater, A. J., J. A. Marchant, and J. Vuorinen. 1977. Guide to the identification and ageing of Holarctic waders. British Trust for Ornithology field guide no. 17. BTO, Tring, U.K.

Purvis, A., and A. Rambaut. 1995. Comparative analysis by independent contrasts (CAIC). Vers. 2. Oxford University, Oxford, U.K.

Reynolds, J. D., and P. H. Harvey. 1994. Sexual selection and the evolution of sex differences. Pp. 53–70 *in* R. V. Short and E. Balaban, eds. The differences between the sexes. Cambridge Univ. Press, Cambridge, U.K.

Reynolds, J. D., and T. Székely. 1997. The evolution of parental care in shorebirds: life histories, ecology and sexual selection. Behav. Ecol. 8:126–134.

Saether, B.-E., J. A. Kålås, L. Løfaldli, and R. Andersen. 1986. Sexual size dimorphism and reproductive ecology in relation to mating system in waders. Biol. J. Linn. Soc. 28:273–284.

Sandercock, B. K. 1998. Assortative mating and sexual size dimorphism in Western and semipalmated sandpipers. Auk 115: 786–791.

Selander, R. K. 1972. Sexual selection and dimorphism in birds. Pp. 180–230 *in* B. Campbell, ed. Sexual selection and the descent of man, 1871–1971. Aldine, Chicago, IL.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quart. Rev. Biol. 64: 419–442.

Sibley, C. G., and J. E. Ahlquist. 1990. Phylogeny and classification of birds. Yale Univ. Press, New Haven, CT.

Székely, T., and J. D. Reynolds. 1995. Evolutionary transitions in parental care in shorebirds. Proc. Roy. Soc. Lond. B. 262:57–64.

Tarboton, W. R., and C. H. Fry. 1986. Breeding and other behaviour of the lesser jacana. Ostrich 57:233–243.

Temeles, E. J., and W. M. Roberts. 1993. Effect of sexual dimorphism in bill length on foraging behavior: an experimental analysis of hummingbirds. Oecologia 94:87–94.

Tomkovich, P. S. 1989. Parental roles and the mating system of the long-toed stint *Calidris subminuta.* Wader Study Group Bull. 57:42–43.

Urban, E. K., C. H. Fry, and S. Keith. 1986. The birds of Africa. Vol. II. Academic Press, London.

Walters, J. R. 1982. Parental behavior in lapwings (Charadriidae) and its relationships with clutch sizes and mating systems. Evolution 36:1030–1040.

Weatherhead, P. J., and K. L. Teather. 1994. Sexual size dimorphism and egg-size allometry in birds. Evolution 48:671–678.

Zar, J. H. 1996. Biostatistical analysis. Prentice-Hall International, London.

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APPENDIX 1

Data used in the analyses and data sources. MG, socially monogamous; PG, socially polygynous; PA, socially polyandrous; AC, acrobatic aerial display; NA, nonacrobatic aerial display; GR, ground display. See text for explanation of parental care scores. References: (1) Blake 1977; (2) Byrkjedal et al. 1997; (3) Colston and Burton 1988; (4) Cramp and Simmons 1983; (5) Cramp 1985; (6) Dunning 1993; (7) Higgins and Davies 1996; (8) del Hoyo et al. 1996; (9) Jehl 1973; (10) Jehl and Murray 1986; (11) Jenni and Collier 1972; (12) Johnsgard 1981; (13) MacLean 1969; (14) Marchant and Higgins 1993; (15) Myers et al. 1982; (16) Oliver 1955; (17) Pitelka et al. 1974; (18) Poole and Gill 1992; (19) Prater et al. 1977; (20) Saether et al. 1986; (21) Székely and Reynolds 1995; (22) Tarboton and Fry 1986; (23) Tomkovich 1989; (24) Urban et al. 1986; (25) Walters 1982.

Species	Body mass (g)		Wing length (mm)		Bill length (mm)		Mating system	Display	Care duration		References
	Male	Female	Male	Female	Male	Female			Male	Female	
Aphriza virgata	186.8	216.3	171.8	178.8	24.1	26.5	MG	AC	7	7	8, 18
Arenaria interpres	108	113	155	157	22.4	22.8	MG	AC	7	4	4, 10, 21
Attagis gayi			191	191.3	23.8	24.3	MG				1, 8
Burhinus grallarius	671.5	625.3	278.8	272	49.2	48.7	MG	GR	7	7	14, 21
Calidris acuminata	70.3	63.5	140	130	26.3	24.7	PG	NA	0	7	3, 4, 12, 17, 21
Calidris alba	52.8	55.4	125	130	25.6	26.4	MG	AC	7	0	4, 21
Calidris alpina	41	45.1	112	116	26.1	29.5	MG	AC	6	4	4, 21
Calidris bairdii	39.3	39.7	125	129	22.3	23.8	MG	AC	7	4	4, 10, 17, 21
Calidris canutus	126	148	169	173	32.6	34.4	MG	AC	7	6	4, 21
Calidris ferruginea	63.2	63.3	132	133	36.2	40.1	PG	AC	0	7	4, 10, 17, 21
Calidris fuscicollis	39.7	45.8	122	125	23.2	24.4	PG	AC	0	7	4, 16, 18, 21
Calidris maritima	67.6	76.3	127	132	27.5	32	MG	AC	7	3	3, 4, 10, 21
Calidris mauri	28	31	97.1	101	23.1	26.7	MG	AC	7	4	3, 4, 7, 10, 17, 21
Calidris melanotos	97.8	65.1	144	131	29.6	27.7	PG	NA	0	7	4, 10, 17, 21
Calidris minutilla	20.3	22.2	89.8	91.6	18.2	19.5	MG	AC	7	5	4, 18, 21
Calidris ptilocnemis	76.3	83	121.3	125.5	26.8	29.8	MG	AC	7	4	6, 15, 19
Calidris pusilla	25	27	95.9	100.1	18.6	20.2	MG	AC	6	5	3, 4, 10, 17, 21
Calidris ruficollis	25.7	26.6	103.5	106.2	17.5	18.7	MG	AC	7	4	3, 4, 10, 17, 21
Calidris subminuta	29	32	93.1	95	17.8	18.8	MG	AC	7	4	4, 15, 23
Calidris tenuirostris	156	174	185	192	42.1	43.8	MG	AC	7	3	4, 15
Catharacta maccormicki	1277	1421	410	415	49.4	50.9	MG	AC	7	7	7
Cepphus grylle	376	380	160	160	29.8	29.8	MG	GR	7	7	5
Charadrius alexandrinus	48.2	47.1	111	112	15.4	15.2	PA	NA	7	4	4, 21
Charadrius dubius	38.3	39.2	117	116	12.7	12.9	MG	NA	7	4	4, 21
Chionis alba	735	638	253	242	34.4	32	MG	GR	7	7	14, 21
Coenocorypha aucklandica	101.2	116.1	106.2	109.2	57.5	60.9	PG	AC	7	7	7, 21
Coenocorypha pusilla	75.9	85.4	99.9	100.5	43.6	44.4	MG	AC	7	7	7, 21
Dromas ardeola			215	215	58.1	56.8		GR			4, 10
Eudromias morinellus	100	117	151	155	15.9	16.8	PA	NA	7	0	4, 21
Fratercula arctica	398	368	165	161.4	46.1	43.4	MG	GR	7	7	5
Gallinago gallinago	111	128	134	134	66.6	68.5	MG	AC	7	7	4, 21
Gallinago media	155	175	144	146	61.2	64.7	PG	GR	0	7	4, 10, 20, 21
Glareola maldivarum	76.8	75.2	185.2	182.9	15.1	15.5	MG	NA	7	7	7, 10, 21
Haematopus ostralegus	500	536	254	255	69.6	78.4	MG	AC	7	7	4, 10, 21, 24
Himantopus himantopus	164	157	247	232	63.7	61.1	MG	NA	7	7	4, 14, 21
Irediparra gallinacea	84	143	121.8	141.1	25.4	29.2	PA	GR	7	0	8, 14, 21
Jacana spinosa	86.9	145.4	120.3	135.3	17.8	19.3	PA	GR	7	0	1, 8, 11, 21
Larus argentatus	977	813	425	404	53.2	48.9	MG	GR	7	7	4
Larus minutus	99	98	225	218	22	21.8	MG	NA	7	7	4
Limicola falcinellus			105	110	30.4	33.5	MG	AC	7	4	4, 7
Limosa limosa	264	315	207	218	92.1	107	MG	AC	7	7	4, 21
Micropalama himantopus	55.8	60.4	132	134	39.5	41.3	MG	AC	7	4	4, 9, 17, 21
Microparra capensis			86.8	90.6	15.6	16.2	MG	GR	7	7	21, 22, 24
Numenius arquata	662	788	292	310	118	137	MG	AC	7	6	4, 21
Pedionomus torquatus	54	72.4	88.9	96.5	12.3	12.8	PA	GR	7	0	14, 21
Phalaropus lobatus	32.4	37.4	108	114	21.1	21.4	PA	NA	7	0	4, 21
Philomachus pugnax	199	118	191	158	35	30.9	PG	GR	0	7	4, 21
Pluvialis apricaria	175	176	190	190	21.8	21.6	MG	NA	7	6	4, 21
Pterocles orientalis	428	383	237	228	13.4	13.4	MG		7	7	5
Recurvirostra avosetta			226	225	86.1	78.3	MG	GR	7	7	4, 21
Rostratula benghalensis	146	159	129.4	139.7	48.9	50.6	PA	GR	7	0	4, 14, 21
Rostratula semicollaris			103.9	107	42.3	42.7	MG		7	7	1, 8, 21
Scolopax minor	168.4	210.5	128	142	63.9	71.5	PG	AC	2	7	10, 18, 21
Scolopax rusticola	306	313	202	200	70.9	73.5	PG	NA	0	7	4, 21
Sterna hirundo	124	126	272	270	37.1	35.2	MG	NA	7	7	5
Stiltia isabella	66	65	203.3	194.7	17.2	16.7	MG	GR	7	7	7
Thinocorus rumicivorus	49	60	114	115.6	14	14.3	MG	NA	0	7	1, 10,13
Tringa hypoleucos	45.5	50	112	112	24.6	24.5	MG	NA	7	5	4, 21
Tringa macularia	36.9	48	105	109	23.2	24.1	PA	GR	7	0	4, 10, 21
Tringa totanus	123	135	159	161	41.7	42.7	MG	AC	7	6	4, 21
Tryngites subruficollis	70.5	53	136	129	20.1	18.5	PG	GR	0	7	4, 10, 17
Uria aalge	1007	994	212	216	49.4	46.6	MG	GR	7	7	5
Vanellus spinosus	191.5	183.8	203	200.7	27.2	26.7	MG	NA	7	7	4, 21, 25
Vanellus vanellus	211	226	229	224	24.1	23.9	PG	AC	7	6	2, 4, 21

APPENDIX 2

Species pairs that differ in (a) mating system; (b) display type; and (c, d) the duration of biparental care. For display type (b) and the duration of biparental care (d), we chose species pairs in which the social mating system was similar between species of a given pair.

a.

More polygynous	More polyandrous
Microparra capensis	*Irediparra gallinacea*
Scolopax minor, S. rusticola	*Jacana spinosa*
Rostratula semicollaris	*Rostratula benghalensis*
Thinocorus rumicivorus, Attagis gayi	*Pedionomus torquatus*
Coenocorypha aucklandica	*Coenocorypha pusilla*
Gallinago media	*Gallinago gallinago*
Tringa totanus	*Phalaropus lobatus*
Tringa hypoleucos	*Tringa macularia*
Philomachus pugnax	*Aphriza virgata, Calidris tenuirostris, C. canutus*
Calidris acuminata	*Limicola falcinellus*
Calidris ferruginea	*Calidris subminuta, C. ruficollis*
Tryngites subruficollis	*Calidris ptilocnemis, C. maritima, C. alpina*
Calidris melanotos	*Calidris pusilla, C. mauri*
Calidris fuscicollis	*Calidris minutilla*
Vanellus vanellus	*Vanellus spinosus*
Charadrius dubius	*Charadrius alexandrinus*
Pluvialis apricaria	*Eudromias morinellus*

b.

Less acrobatic display	More acrobatic display	Mating system
Microparra capensis	*Thinocorus rumicivorus*	monogamous
Scolopax rusticola	*Scolopax minor*	polygynous
Gallinago media	*Coenocorypha aucklandica*	polygynous
Tringa hypoleucos	*Tringa totanus*	monogamous
Philomachus pugnax	*Calidris acuminata*	polygynous
Tryngites subruficollis	*Calidris ferruginea*	polygynous
Calidris melanotos	*Calidris fuscicollis*	polygynous
Recurvirostra avosetta	*Haematopus ostralegus*	monogamous
Burhinus grallarius	*Pluvialis apricaria*	monogamous
Stiltia isabella	*Glareola maldivarum*	monogamous
Sterna hirundo	*Catharacta maccormicki*	monogamous
Larus argentatus	*Larus minutus*	monogamous

c.

Less biparental	More biparental
Jacana spinosa	*Pterocles orientalis*
Irediparra gallinacea	*Microparra capensis*
Rostratula benghalensis	*Rostratula semicollaris*
Pedionomus torquatus, Thinocorus rumicivorus	*Coenocorypha aucklandica, C. pusilla*
Scolopax rusticola	*Scolopax minor*
Gallinago media	*Gallinago gallinago*
Phalaropus lobatus	*Limosa limosa*
Tringa macularia	*Tringa hypoleucos*
Philomachus pugnax	*Arenaria interpres*
Calidris tenuirostris	*Aphriza virgata*
Calidris acuminata	*Limicola falcinellus*
Calidris ferruginea	*Calidris subminuta, C. ruficollis*
Calidris maritima	*Calidris ptilocnemis*
Tryngites subruficollis	*Calidris alpina*
Calidris mauri	*Calidris pusilla*
Calidris melanotos	*Calidris bairdii*
Calidris fuscicollis	*Calidris minutilla*
Vanellus vanellus	*Vanellus spinosus*
Eudromias morinellus	*Pluvialis apricaria*

d.

Less biparental	More biparental	Mating system
Thinocorus rumicivorus	*Microparra capensis, Rostratula semicollaris*	monogamous
Scolopax rusticola	*Scolopax minor*	polygynous
Gallinago media	*Coenocorypha aucklandica*	polygynous
Numenius arquata	*Limosa limosa*	monogamous
Tringa hypoleucos	*Tringa totanus*	monogamous
Calidris tenuirostris	*Aphriza virgata*	monogamous
Calidris maritima	*Calidris ptilocnemis*	monogamous
Calidris mauri	*Calidris pusilla*	monogamous
Calidris alba	*Calidris minutilla*	monogamous
Charadrius dubius	*Vanellus spinosus*	monogamous
Pluvialis apricaria	*Haematopus ostralegus, Himantopus himantopus, Recurvirostra avosetta*	monogamous