



A comparative study on the evolution of reversed size dimorphism in monogamous waders

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Sexual dimorphism in size is common in birds. Males are usually larger than females, although in some taxa reversed size dimorphism (RSD) predominates. Whilst direct dimorphism is attributed to sexual selection in males giving greater reproductive access to females, the evolutionary causes of RSD are still unclear. Four different hypotheses could explain the evolution of RSD in monogamous birds: (1) The 'energy storing' hypothesis suggests that larger females could accumulate more reserves at wintering or refuelling areas to enable an earlier start to egg laying. (2) According to the 'incubation ability' hypothesis, RSD has evolved because large females can incubate more efficiently than small ones. (3) The 'parental role division' hypothesis suggests that RSD in monogamous waders has evolved in species with parental role division and uniparental male care of the chicks. It is based on the assumption that small male size facilitates food acquisition in terrestrial habitats where chick rearing takes place and that larger females can accumulate more reserves for egg laying in coastal sites. (3) The 'display agility' hypothesis suggests that small males perform better in acrobatic displays presumably involved in mate choice and so RSD may have evolved due to female preference for agile males. I tested these hypotheses in monogamous waders using several comparative methods. Given the current knowledge of the phylogeny of this group, the evolutionary history of waders seems only compatible with the hypothesis that RSD has evolved as an adaptation for increasing display performance in males. In addition, the analysis of wing shape showed that males of species with acrobatic flight displays had wings with higher aspect ratio ($\text{wing span}^2/\text{wing area}$) than non-acrobatic species, which probably increases flight manoeuvrability during acrobatic displays. In species with acrobatic displays males also had a higher aspect ratio than females although no sexual difference was found in non-acrobatic species. These results suggest that acrobatic flight displays could have produced changes in the morphology of some species and suggest the existence of selection favouring higher manoeuvrability in species with acrobatic flight displays. This supports the validity of the mechanisms proposed by the 'display agility' hypothesis to explain the evolution of RSD in waders.

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INTRODUCTION

In most species of birds males are of the same size or larger than females (Price, 1984). The larger body size of males has been explained as the result of intrasexual competition for mating opportunities (Darwin, 1871; Selander, 1972). However, in some species of waders, diurnal raptors, owls and other birds, females are larger than males. While reversed size dimorphism (RSD) of polyandrous species could be explained as the result of female competition for breeding resources (mates, territories or breeding sites), its evolutionary origin in monogamous species remains unclear (Jehl & Murray, 1986, 1989; Mueller, 1989, 1990). Several hypotheses have been proposed to explain the occurrence of RSD. Some suggest that it evolved to reduce the intensity of intersexual competition on the breeding grounds and reduce the size of feeding territories used and defended by the members of a pair ('ecological hypotheses') (Selander, 1966, 1972; Ashmole, 1967). Thus pairs of individuals of different sizes could exploit a wider ecological niche than monomorphic pairs. However, as Mueller (1990) pointed out, ecological hypotheses usually fail to predict the direction of the dimorphism (i.e. which sex should be larger than the other). Jönsson and Alerstam (1990) proposed a hypothesis that combines sexual differences in habitat use and parental care, that would explain on its own the direction and intensity of size dimorphism (see below).

Reproductive hypotheses argue that RSD is the result of selection favouring (1) larger females that lay large eggs (Selander, 1972) and/or possess greater incubation abilities (Snyder & Wiley, 1976), or (2) smaller but more agile males in species that perform acrobatic flight displays before and during pair formation (Jehl & Murray, 1986).

Some of these hypotheses have been tested by comparing the life-histories of different species. In these previous works there has been no attempt to account for the effects of phylogeny (Ross, 1979; Mueller & Meyer, 1985; Jehl & Murray, 1986; Saether *et al.*, 1986; Jönsson & Alerstam, 1990; but see Olsen & Cockburn, 1993). Data from different species may not be independent from each other, since some species could have similar characteristics as a result of sharing a common ancestor, rather than being the results of similar ecological or behavioural selection pressures. The direct comparison of data from different species increases the risk of obtaining erroneous results (Harvey & Pagel, 1991; Harvey, 1996), because the existence of phylogenetic relationships between the species increases the risk of a type I statistical error.

The aim of this paper is to test the hypotheses proposed to explain the evolution

of RSD in monogamous birds, taking into account the effects of phylogeny. This paper focuses on waders (order Charadriiformes) because this group includes species with both normal and reversed dimorphism that exceeds the range of size dimorphism found in other families of birds (Jehl & Murray, 1986). Of the important hypotheses proposed up to now (reviewed in Jehl & Murray, 1986; Mueller, 1990), I have tested those that could successfully predict the direction of the dimorphism (i.e. which sex should be larger). I have not considered those hypotheses that only predict the existence rather than the direction of these differences, because they could not successfully explain the patterns of RSD in birds (see reviews by Jehl & Murray, 1986; Mueller, 1990).

The hypotheses and their predictions

The hypotheses I set out to test in this paper can be divided into two main groups according to the advantages derived by each sex.

Selection favouring large females

(1) *Large egg size.* Selander (1972) suggested that large female size could facilitate the formation of large eggs. The possible advantage of this is that large eggs hatch large chicks and large chicks tend to survive better than small ones (Galbraith, 1988; Grant, 1991). This hypothesis predicts that species with RSD should lay larger eggs than species without or with normal dimorphism. However, Olsen & Cockburn (1993) and Weatherhead & Teather (1994) analysed the patterns of size dimorphism, body and egg mass in waders and other birds and did not find any supporting evidence. Consequently, I have not further considered this hypothesis.

(2) *Energy storing.* This hypothesis is based on the idea that species breeding in the Arctic during egg laying use the energetic reserves accumulated in their wintering or refuelling areas (Downhower, 1976). Large females can carry large body reserves to the breeding grounds and may benefit from early breeding or lay larger clutches (Jehl & Murray, 1986). However, there is little evidence to suggest that waders carry significant reserves to the breeding grounds to be used in egg formation (see Erckmann, 1983). This hypothesis predicts a relationship between mean breeding range and size dimorphism in body mass, with RSD predominating in species breeding at higher latitudes.

(3) *Efficient incubation.* This hypothesis was proposed to explain the patterns of size dimorphism in raptors (Snyder & Wiley, 1976). These authors suggested that large females can cover and warm the eggs more efficiently than small ones. Puttick (1981) also suggested that in the curlew sandpiper (*Calidris ferruginea*) females are larger than males because females are responsible for incubation. According to this hypothesis, RSD in body mass should predominate in the species where females have a larger share in incubation than males. It should not occur in species with shared or male-preponderant incubation because in these later species selection for increased incubation efficiency would be the same for each sex or even stronger in males. Shared incubation is the most parsimonious ancestral state in waders (Székely & Reynolds, 1995), so the reconstruction of the evolution of incubation patterns should indicate that female uniparental incubation evolved before or at the same time as RSD. This kind of test relies on the idea that the factor responsible for the

evolution of RSD should occur in each one of the evolutionary moments of its appearance (see Björklund, 1991).

Selection favouring small males

(1) *Efficient foraging during brood rearing* ('parental role division' hypothesis). Jönsson and Alerstam (1990) suggested that RSD in waders is associated with male uniparental care or with a great share of males in brood rearing. According to this hypothesis, males are the smaller sex because small body size reduces the energetic costs of parental care. In addition, a short bill was assumed to increase foraging efficiency during brood rearing in species that feed by deep probing but which take care of the brood in terrestrial habitats where prey has to be pecked from the soil surface (see discussion in Jönsson, 1987). Jönsson & Alerstam (1990) also suggested that larger female size should confer advantages in the accumulation of more reserves for egg production and increased foraging efficiency in coastal habitats (see Burton, 1974; Jönsson, 1987). This hypothesis predicts an inverse relationship between the degree of size dimorphism and male share in parental care, with RSD predominating in species with male uniparental care.

(2) *Greater agility in courtship displays* ('display agility' hypothesis). Hovering is very important in the acrobatic displays, and models of flight costs show that hovering is a very energetically expensive activity that may be cheaper for smaller males (Peters, 1983). This hypothesis rests upon the assumption that, in the same way that sexual selection can promote the development of energetically costly structures or behaviours, selection could favour morphological or behavioural adaptations in reducing these costs and increasing display performance. In species where males perform song flights, this behaviour is associated with the evolution of changes in wing morphology that reduce the cost of song flights, and allow longer displays without an increase in the energy allocated to defence of breeding resources and mate attraction (Miller, 1991; Hedenström & Møller, 1992; Grønstøl, 1996). In the same way, males of species with long tails develop larger wings presumably to cope with the increased aerodynamic costs of this trait (Andersson & Andersson, 1994; Balmford, Jones & Thomas, 1994). These recent studies have shown that the reduction of display costs could be an important selective force modelling bird morphology. In this way, Jehl & Murray (1986) suggested that the increase of acrobatic flight performance during sexual displays and consequently the reduction of its energetic costs, could be the primary selective force promoting the evolution of RSD in waders. This hypothesis is based on the assumption that manoeuvrability is an important component of these displays and that more agile males dominate over other displaying individuals or were preferred by females (see Grønstøl, 1996). The 'display agility' hypothesis predicts that RSD in body mass should predominate in species performing acrobatic flight displays and that its evolution occurred at the same time or after the appearance of acrobatic flights in each clade. However, no differences in wing and tail dimorphism were expected between species with and without acrobatic flight displays, as larger wings also increase flight manoeuvrability (Hedenström & Møller, 1992). Tail length seem to play an important role during the performance of some acrobatic aerial displays, in which males spread the feathers of the tail during the descent phases of display flights (see Miller, 1984). These two last predictions are limited by the fact that morphological characters do not evolve independently of each other (Schluter, 1989; Björklund & Merila, 1993) so it is

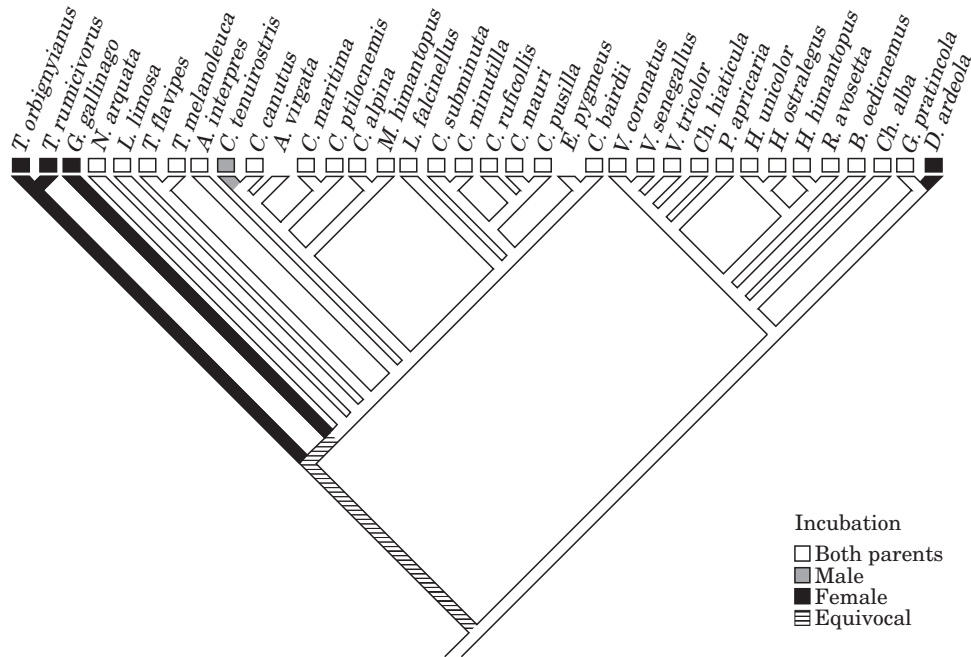


Figure 1. Phylogenetic distribution of incubation behaviour in waders.

possible that manoeuvrability may not have been maximized in all the different characters implied in flight performance. Nevertheless, it should be expected that differences in sexual dimorphism in wing and tail length between acrobatic and non acrobatic species will be less noticeable than in body mass. Additionally, I have examined the wing morphology of different species to test the hypothesis that species with acrobatic flight displays have evolved mechanisms or structures to reduce the costs and increase the performance during the sexual displays. The aim of this test was to confirm the existence of selection for increased male agility in species with acrobatic flight displays to support the assumptions of ‘display agility’ hypothesis.

MATERIAL AND METHODS

To determine the relationships within the Charadrii I used the mitochondrial DNA-DNA hybridization phylogeny of Sibley & Ahlquist (1990). The relationships within Calidrine sandpipers were established according to Van Rhijn’s (1990, 1991) phylogeny, constructed using morphological and biogeographical data. These two different sources were combined to construct the working phylogeny used in this paper (Fig. 1). Székely & Reynolds (1995) assembled a phylogeny which includes a large number of species. Nevertheless, their phylogeny presented numerous unresolved polytomies (multiple speciation events that reflect a lack of knowledge of the detailed radiation of these species) and a greater uncertainty in the lengths of the branches in different parts of the tree. While some of the comparative methods used in this paper can deal with tree uncertainties, others cannot and so I chose to use a reduced, but fully resolved, phylogeny. The biology of some species enclosed

in Sibley and Ahlquist's phylogeny was poorly known and so these species were not included in the analyses. In order to remove unresolved polytomies from the phylogeny only one of the species randomly included in each unresolved node was considered in the analyses.

The data used in these analyses were obtained from different bibliographic sources (Appendix). When available, I selected data from breeding birds. Size dimorphism was calculated as the ratio of mean male over mean female measurements. For each character, the dimorphism of a species was classified as reversed when the ratio was equal or lower than 0.95 (reflecting a difference of 5% in the size of the character). Species with ratios equal or greater than 1.05 were considered to show direct dimorphism, while the remaining species were considered non-dimorphic. These cut-off points avoided considering as dimorphic such species with small sexual differences in the measurements listed in the Appendix, which are probably without statistical biological significance. I analysed separately the patterns of size dimorphism in wing, tail and bill length and body mass, because these are the morphological variables involved in the evolution of reversed dimorphism according to different hypotheses and have been discussed extensively by the authors listed in the Appendix. The different hypotheses suggest that RSD has evolved by selection acting on some particular character (e.g. selection for dimorphism in body mass) and that the overall dimorphism in other characters is due to the correlated evolution of morphological characters or evolutionary constraints (i.e. Jehl & Murray, 1989). According to this view, I have tested each hypothesis using only the characters affected by the mechanisms proposed in each case to explain the evolution of RSD. Relative parental care of male vs. female was scored for each species according to the seven categories defined in Jönsson & Alerstam (1990):

“category 1, incubation and brood-rearing by female alone; male takes no part in parental care; 2, female incubates alone but brood is later divided and cared for by both sexes; 3, male and female share incubation and brood-rearing more or less equally; 4, incubation shared more or less equally, but female leaves the family during the second half of the fledging period; 5, incubation shared more or less equally, but female leaves the family during the first half of the fledging period; 6, incubation by both sexes at first, but female leaves a few days before hatching and subsequent brood-rearing is by the male alone; 7, incubation and brood rearing is by the male alone, female takes no part in parental care.”

Incubation behaviour was derived from this classification: species with codes 1 and 2 were classified as having a preponderance of female incubation; codes 3 to 5 corresponded to shared incubation; and species with codes 6 and 7 were classified as showing a preponderance of male incubation. Sexual displays were classified as acrobatic and non-acrobatic, according to Jehl & Murray (1986) or from the descriptions reported in Cramp & Simmons (1983) and Marchant & Higgins (1993). No distinction was made between mate attraction and territorial displays by two reasons: (1) for most of the cases there is no information to ascertain the exact display function; (2) a higher performance in territorial displays will also result in a selection favouring higher manoeuvrability in males. Acrobatic displays include abundant steep dives and climbs, twists and turns. The ability to perform these turns increases with low minimum turning radius and high minimum gliding speed,

aerodynamic parameters affected negatively by increases in body mass (Hedenström & Møller, 1992). Among species without acrobatic flight displays I considered species without aerial displays, such as the stone curlew *Burhinus oedicnemus*, as well as others that perform flight displays, but without any noticeable acrobatic component, for example the 'butterfly' display common in plovers (genus *Charadrius*), (see Jehl & Murray, 1986).

Phylogenetic analyses

Felsenstein's (1985) method of pairwise independent comparisons was used to examine the relationships between different continuous variables. The independent comparisons method calculates statistics among clades by making successive comparisons of each pair of lineages from each node in the tree. The logic of this method relies on the fact that although data from different species were not statistically independent, pairwise contrasts between the values of related lineages were independent in terms of the evolutionary changes that occurred in the other contrasts of the tree (Harvey & Pagel, 1991; Garland, Harvey & Ives, 1992). These contrasts were standardized in relation to the time elapsed since the separation of the lineages in the tree by using branch lengths. I tested the suitability of branch length standardization by examining the correlation between the absolute value of the standardized independent contrasts and its standard deviations. A significant correlation was detected for dimorphism ratios and mean breeding latitude, indicating that branch lengths were inadequate for standardizing these contrasts (Garland *et al.*, 1992). In these cases, branch lengths were cube root transformed, thus removed all significant correlations. Relationships between variables were examined using linear regression through the origin of the standardized independent contrasts. When contrasts were derived from discrete variables (in the case of analyses with the categories of relative importance of male parental care), the Kendall rank correlation was used to examine the relationships with the contrasts of other variables. To determine if different selective forces were operating on different characters, I examined the correlations of the intensity of dimorphism in two different variables (see Lundberg, 1986)—bill length and body mass—since these are the variables implied in most of the hypotheses on the evolutionary causes of reversed size dimorphism proposed to date (Jehl & Murray, 1986; Mueller, 1990).

The differences in the variables analysed between different groups of species were tested with ANOVA (Garland *et al.*, 1993). Given the non-independence of species data, due to the effect of a common ancestor, I used computer simulations to calculate the null distribution of *F*-statistics. The evolution by Brownian motion (the variations of a trait occurring randomly and independently from the size of the trait; Felsenstein, 1985) of the characters analysed was simulated on 1000 occasions along the untransformed phylogenetic tree. *F*-statistics were computed for each of these simulations and 95% confidence limits were established as the 95 percentiles from the distributions of the *F*-statistics of the simulations. Initial values for size dimorphism were obtained from the independent contrast for the root node (bill dimorphism = 0.98, body mass and wing length dimorphism = 1.00, tail dimorphism = 1.01), these values being equivalent to those obtained by the method of minimum evolution (Maddison, 1991). To test the robustness of the assumptions of the evolution of size dimorphism, I repeated a simulation analysis for each data set under four different

combinations of phenotypic correlations and models of evolutionary change. The evolution of dimorphism in wing, tail and bill length was assumed to be correlated with dimorphism in body mass ($r=0.80$, 0.68 and 0.77 respectively, values that correspond to the correlation of the species tip data) or uncorrelated ($r=0$). Altogether, in these simulations, expected variance of change was assumed to be proportional to branch length (gradual model) or to be the same for each branch (speciation model). For each simulation, the evolution of dimorphism was restricted between a lower bound of 0.5 (females twice the size of males) and upper bound of 2.0 (males twice the size of females). The simulated values were restricted within these ranges using the soft-bound algorithm (Garland *et al.*, 1993). With this algorithm it is harder to move towards a boundary than away from it, and it is harder to move towards a boundary when the trait is near it than when the trait is far from it. In addition, a trait could not move more than the half of distance to a boundary in a single step. With these restrictions, no character could surpass the boundaries fixed during simulations.

A detailed description of the base-line and methodology of these analyses can be found in Felsenstein (1985), Harvey & Pagel (1991) and Garland *et al.* (1993). The computer program PDAP (Garland *et al.*, 1993) was used to calculate independent contrasts, as well as ANOVA. The contingent states test (Sillén-Tullberg, 1993) was used to evaluate the null hypothesis that change from non-dimorphism to reversed dimorphism in one branch was independent of the values of other variables in that branch. The reconstruction of the evolution of discrete variables was performed using MacClade 3.01 (Maddison & Maddison, 1992). Incubation behaviour at the ancestral node could not be reconstructed unequivocally with this method and I assumed that the ancestral shorebird showed incubation by both sexes (see Székely & Reynolds, 1995). Although data of the body masses of *Thinocorus sp.* are almost totally lacking, in the reconstruction of the evolution of body mass dimorphism, I also assumed that these species were not dimorphic because they were non-dimorphic in bill and in other characters like wing, tail and tarsus (Blake, 1977). Additional assumptions of the comparative methods used in this study are: (a) within-species variation is negligible compared to between-species variation, (b) the evolutionary changes in discrete characters are relatively rare and uniformly distributed over the branches, (c) the process of phenotypic evolution of continuous characters can be described as a Brownian motion process, and (d) the rate of phenotypic evolution is constant over the clade (see Martins & Hansen, 1996).

Wing shape analysis

Morphological data were collected from museum specimens of four pairs of shorebird species (Table 1). In each pair one species has acrobatic flight and the other has not. According to Gochfeld, Burger & Jehl (1984), species in one of the pairs belonged to the same genera, in another pair to the same tribe and the two other pairs to the same subfamily. I used the pairwise comparative method to control for phylogeny and habitat effects (Møller & Birkhead, 1992). The number of pairs of species analysed was small because it was limited by the scarce occurrence of transitions from non-acrobatic to acrobatic displays in waders (see Results). Due to this small number of transitions I have included in the non-acrobatic group three polygynous and one polyandrous species, while the other four species show a

TABLE 1. Mating system (ms): polyandry (Pa), monogamy (M), polygyny (Pg); type of sexual display (d): acrobatic (Ac), aerial non-acrobatic (Na); mean migration distance in degrees (md) and PC1 and PC2 scores for males and females of each species analysed (mean \pm s.d. and number of individuals measured referred in brackets)

Species	ms	d	md	PC1		PC2	
				males	females	males	females
<i>Tringa stagnatilis</i>	M	Ac	59	-0.01 ± 0.29 (26)	-0.00 ± 0.33 (27)	-0.10 ± 0.39	-0.12 ± 0.32
<i>Actitis hypoleucos</i>	M	Na	60	0.44 ± 0.32 (29)	0.41 ± 0.32 (31)	0.62 ± 0.37	0.66 ± 0.27
<i>Limnocyptes minimus</i>	Pg	Ac	48	-0.74 ± 0.26 (23)	-0.59 ± 0.37 (28)	2.02 ± 0.20	2.17 ± 0.26
<i>Scolopax rusticola</i>	Pg	Na	10	1.89 ± 0.55 (33)	1.82 ± 0.65 (33)	-0.18 ± 0.41	-0.08 ± 0.39
<i>Limosa limosa</i>	M	Ac	40	-0.63 ± 0.68 (4)	-0.40 ± 0.20 (4)	-1.24 ± 0.47	-1.56 ± 0.51
<i>Phalaropus fulicarius</i>	Pa	Na	71	-0.56 ± 0.33 (28)	-0.52 ± 0.30 (26)	-0.49 ± 0.34	-0.58 ± 0.28
<i>Calidris canutus</i>	M	Ac	84	-1.08 ± 0.30 (33)	-0.94 ± 0.26 (24)	-0.76 ± 0.35	-0.86 ± 0.31
<i>Calidris melanotos</i>	Pg	Na	100	-0.44 ± 0.28 (27)	-0.42 ± 0.24 (27)	-0.86 ± 0.32	-0.82 ± 0.34

predominantly monogamous mating system. To control for possible effects of mating system, none of the two groups was biased towards a particular system, and half of the comparisons were established between species with the same mating patterns.

I measured the length of the third primary from the tip to its insertion in the wing (to the nearest 0.5 mm), and the distance from the tip of the wing to the tip of each of the eight distal primaries (the outer relictual primary was not considered owing to its small size in waders). Distances to the tip of the wing were transformed to primary lengths by subtracting distance to the tip from the length of the longest primary. The sex of the bird was registered from the labels of the specimens, because reliable sexing methods based on plumage characteristics were not available for the studied species (Prater, Marchant & Vuorinen, 1977). Birds were aged according to plumage and moult patterns (Prater *et al.*, 1977), except for jack snipe *Limnocyptes minimus* due to the difficulty of age determination. Data of first-year birds were not considered because age-related differences in wing shape seems to occur in some birds (Senar, Lleó & Metcalfe, 1994; and references therein), and these differences would have hidden sexual or interspecific differences in wing shape. To analyse wing shape I used principal component analysis (PCA) of primary lengths. The first eigenvector of PCA used to be associated with an overall size axis (Cuadras, 1981; Rising & Somers, 1989). However, the differences in overall size within or between species were outside the scope of this study, especially when the species studied differ widely in body size. This made it necessary to remove the effect of body size on primary length. The method of Senar *et al.* (1994) was used to correct primary lengths to the values of a standard individual with a length of the longest primary of 110 mm. Standardization parameters were calculated separately for each species, since the allometric relationships between primary lengths and size could be different for each species (J.C. Senar, unpublished). Migration distances were calculated as the difference in degrees between mean breeding and wintering latitudes from the distribution maps in Cramp & Simmons (1983) and Hayman, Marchant & Prater (1986). Differences between acrobatic and non-acrobatic species were tested with the Wilcoxon matched-pairs signed-rank test, and mean \pm SD were reported through this paper.

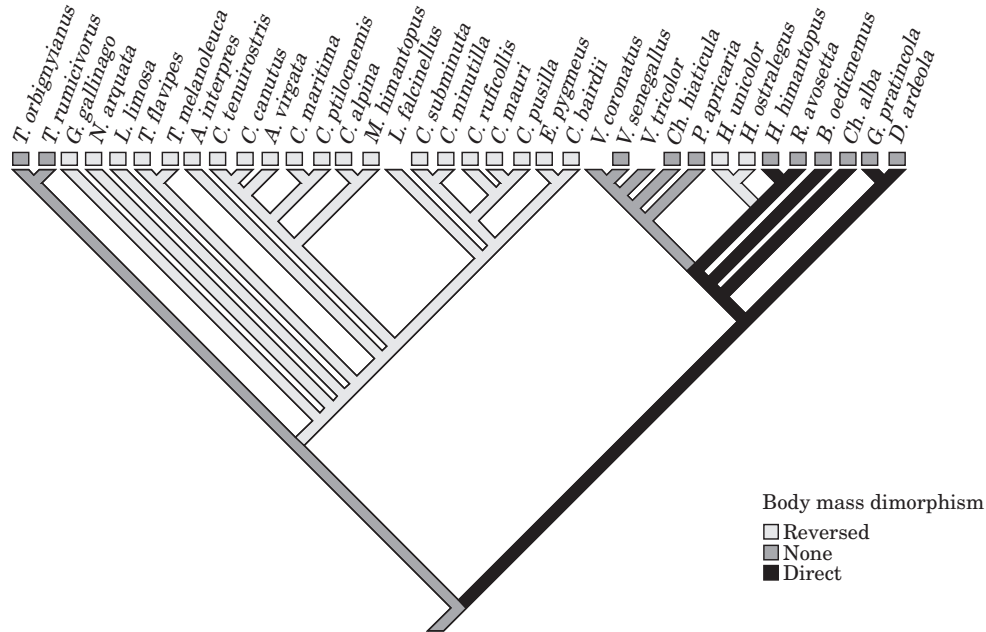


Figure 2. Phylogenetic distribution of body mass dimorphism in waders.

RESULTS

Intensity of sexual dimorphism in bill length was positively correlated with dimorphism in body mass ($r=0.74$, $F_{1,28}=34.16$, $P<0.0001$), suggesting that different selective forces have not affected in opposite directions the degree of size dimorphism in these two characters.

I analysed the relationship between size dimorphism and mean breeding latitude by including only those species that lay clutches of four eggs, in order to remove the possible confusing effect of clutch size. I found no relationships between the degree of size dimorphism in body mass and mean breeding latitude ($r=-0.15$, $F_{1,23}=0.51$, $P=0.48$). To control for the effects of size, the residuals of the regression of dimorphism in body mass vs. males body mass were regressed against mean breeding latitude but, again, no significant relationship was found between dimorphism and latitude ($r=-0.10$, $F_{1,23}=0.23$, $P=0.63$).

The reconstruction of the evolution of incubation patterns (Fig. 1), showed that RSD has evolved once or twice in a clade with shared incubation (Fig. 2), occurring mainly in clades with shared or mainly male incubation, while most of the taxa with female incubation do not exhibit it (Fig. 2). Contingent states test suggest that RSD in body mass has appeared in the tree independently of the kind of incubation system ($P=1.00$).

No relationship was found between relative participation of males in parental care and sexual dimorphism in bill length (Kendall Rank correlation, $\tau=-0.09$, $z=-0.73$, $P=0.46$) or in dimorphism in body mass ($\tau=0.02$, $z=0.14$, $P=0.89$).

Species with acrobatic flight displays showed a higher degree of RSD than non-acrobatic species, with significant differences in the intensity of dimorphism in body

TABLE 2. Means \pm SD of sexual dimorphism in body mass, wing and tail length in species with different kinds of sexual displays. The P -values of ANOVA are reported from the distribution of the F -statistics of 1000 simulations under four different models of evolutionary change

Sexual display	Acrobatic	Non-acrobatic	P
Body mass	0.89 ± 0.039 (20)	1.05 ± 0.084 (8)	0.006–0.010
Wing length	0.97 ± 0.016 (21)	1.01 ± 0.025 (12)	0.058–0.076
Tail length	0.98 ± 0.016 (19)	1.02 ± 0.026 (12)	0.148–0.205



Figure 3. Reconstruction of the evolution of sexual displays in waders. Non-acrobatic displays include species both with terrestrial displays or with aerial but non-acrobatic displays.

mass but not in wing and tail lengths (Table 2). The reconstruction of character evolution indicated that the appearance of reversed dimorphism in body mass (Fig. 2) was clumped around the performance of acrobatic flight displays (Fig. 3). The change from normal to reversed dimorphism in body mass was more probable in branches with species exhibiting acrobatic flight displays ($P=0.003$).

PCA analysis extracted two significant components of wing shape (Table 3). PC1 explained 75% of the variance. The factor scores were similar for all the variables, but negative for the length of the outer primary, representing an axis of increasing central and proximal (P3–P9) and decreasing distal primary length (P2). Thus, I consider that PC1 was inversely related to aspect ratio (wing span²/wing area). PC1 increased with larger wing surface when the effect of wing size (\approx wing span) was controlled, resulting in a decrease of aspect ratio. PC2 explained 16% of the variance and yields high scores for individuals with short central primaries (P4–P5) but especially P3. This component yields low scores for species having long central primaries, resembling a symmetric wing.

TABLE 3. Principal Component Analysis of the length of the eight outer primaries

	Factor loadings	
	PC1	PC2
P2	-0.72	0.04
P3	0.63	-0.76
P4	0.87	-0.44
P5	0.94	-0.24
P6	0.97	0.10
P7	0.93	0.30
P8	0.92	0.38
P9	0.88	0.45
% Variance	75	16
Eigenvalues	5.97	1.28

Species with acrobatic flight displays had lower PC1 scores than non-acrobatic ones, but interestingly differences were only significant for males (males: -0.62 ± 0.45 vs. 0.33 ± 1.13 , $z = 2.01$, $P = 0.04$; females: -0.48 ± 0.39 vs. 0.32 ± 1.08 , $z = 1.64$, $P = 0.10$). PC1 scores of males of species with acrobatic flight displays were lower than females ones (-0.62 ± 0.45 vs. -0.48 ± 0.39 , $z = 2.01$, $P = 0.04$), but no differences were found in species without acrobatic displays (0.33 ± 1.13 vs. 0.32 ± 1.08 , $z = 0.55$, $P = 0.58$). No differences in PC2 scores were found between acrobatic and non-acrobatic species (males: -0.02 ± 1.44 vs. -0.23 ± 0.63 , $z = 0.18$, $P = 0.86$; females: -0.09 ± 1.62 vs. -0.21 ± 0.65 , $z = 0.55$, $P = 0.58$), or between males and females of species with (-0.02 ± 1.44 vs. -0.09 ± 1.62 , $z = 0.91$, $P = 0.36$) or without acrobatic displays (-0.23 ± 0.63 vs. -0.21 ± 0.65 , $z = 0.91$, $P = 0.36$). These results suggest that species performing acrobatic displays have higher aspect ratios (more pointed wings) than non-acrobatic waders, and that sexual dimorphism in aspect ratio is more pronounced in species with acrobatic flight displays. Migration distance, a possible confusing factor in these analyses, did not differ between acrobatic ($57.75^\circ \pm 19.16$) and non-acrobatic species ($60.25^\circ \pm 37.51$, $z = 0.55$, $P = 0.58$).

DISCUSSION

The robustness of the conclusions derived from comparative studies obviously relied on the trustworthiness of the phylogenetic trees used. Future improvements in the knowledge of the phylogenetic relationships between species could thus affect the conclusions derived from these sorts of studies. However, several simulation studies have indicated that the use of phylogenetic comparative methods gives more robust results than non-phylogenetic approaches, even when deficient estimations of branch length or models of evolution were used (Martins & Garland, 1991; Purvis, Gittleman & Luh, 1994; Diaz-Uriarte & Garland, 1996). I tested the validity of four hypotheses proposed to explain the evolution of reversed size dimorphism, using present knowledge of the phylogenetic relations within waders. The type of analyses presented in this paper were not able to demonstrate a relationship of cause-effect between different variables, although they do indicate that only one of the hitherto formulated hypotheses on the evolution of RSD is compatible with the evolution of the patterns of size dimorphism found in monogamous waders. The

predictions of three of the hypotheses were not supported for waders, while there was complete support for the 'display agility' hypothesis. The analysis of the relationships between male involvement in parental care and sexual dimorphism clearly illustrates the problems associated with the analysis of species as independent data points. Jönsson & Alerstam (1990) claimed an inverse relationship between these two variables in an analysis including monogamous and polygamous waders, and I detected negative correlations between parental care and dimorphism in bill length and body mass when analysing the species tip data reported in the present study (Kendall Rank correlation: bill length, $\tau = -0.45$, $z = -3.72$, $P = 0.0002$; body mass, $\tau = -0.35$, $z = -2.63$, $P = 0.009$).

However, none of these correlations remains significant when the effects of phylogeny were accounted for (see Results), suggesting that the relationship between dimorphism and parental care was the spurious result of the phylogenetic relationship between the species analysed and not the result of a functional relationship between these two variables, at least when monogamous species are considered alone (but see Reynolds & Székely, 1997). Additionally, the reconstruction of the evolution of size dimorphism, sexual displays and parental care suggested that only the 'display agility' hypothesis explained successfully the patterns of size dimorphism in monogamous waders. According to Jönsson & Alerstam (1990), in species with RSD, short-billed males remain with the chicks in grasslands, while long-billed females do not usually attend the chicks and instead forage in areas of mudflats where long billed individuals probably forage more successfully (see discussion in Jönsson, 1987). However, while oystercatchers show RSD, both males and females take care for the young, foraging in the same habitat during chick rearing (Cramp & Simmons, 1983), a fact that could reject the validity of the 'parental role division' hypothesis in explaining the evolution of RSD in monogamous waders. This result could be considered as phylogenetically robust, because although the phylogenetic position of some groups of waders is quite controversial, all studies published hitherto have coincided in their conclusions on the position of oystercatchers with respect to calidrine sandpipers and allies (Strauch, 1978; Mickevich & Parenti, 1980; Sibley & Ahlquist, 1990; Björklund, 1994; Chu, 1995) and give little room for alterations of these conclusions as a result of improvements in the knowledge of wader phylogeny. In addition, similar results were obtained when the analyses presented in this paper were repeated using the phylogenies proposed by Chu (1995).

Types of male sexual displays have been shown to affect the morphology of different species of passerines. In terms of energy, flight is the more expensive activity performed by birds, and its cost has been estimated to be ten times the basal metabolic rate (Butler & Woakes, 1990). Additionally, its energetic cost increases allometrically with mass (Andersson & Norberg, 1981; Pennycuik, 1989). Recent works have shown that some sexual differences in the morphology of other birds could have evolved to reduce the costs of energetically expensive sexual displays and increase display performance. In species where song flights are used to attract females, males have an increased wing span, wing area and aspect ratio and reduced wing loading (Møller, 1991; Hedenström & Møller, 1992; M. Andersson, 1994). In passerine species with sexually selected long tails, males have larger wings than females, presumably to reduce the increased aerodynamic costs of their long tails (S. Andersson, 1993; Balmford *et al.*, 1994). All these characteristics would improve display performance, would reduce the magnitude of the energetic costs of the sexual displays, and would allow males to display for longer without increasing the

energy allocated to mate attraction and resource defence. In this way the increased aspect ratio found in males of species with acrobatic flight displays could be interpreted as an adaptation for reducing the energetic costs of sexual displays.

These inter- and intraspecific differences in aspect ratio suggest that selection has favoured increased manoeuvrability in those species supporting the so far untested assumption of Jehl and Murray's hypothesis. Wing shape seems to be correlated with migration distance, pointed wings (and high aspect ratio) predominate in long distance migrants and rounded wings (with low aspect ratios) are typical in short distance migrants and sedentary species (Mönkkönen, 1995). However, no difference was found in migration distance nor in the habitat used by acrobatic and non-acrobatic species analysed. Although it cannot be ruled out that the differences found in wing shape were related to other uncontrolled factors, this possibility seems quite unlikely.

According to the results of this study, RSD of monogamous waders could be considered an adaptation to reduce the energetic cost of the sexual acrobatic flight displays performed by the males of these species. Nevertheless, Andersson (1994) stated that RSD has not evolved in all the species that perform flight displays. However, flight performance seems to be determined by several different components that could not be maximized at once (see Table 1 in Hedenström & Møller, 1992). The displays used by different species differ widely in their structure and acrobatic components so it is likely that the most important factors of aerodynamic performance for display performance are different in terms of the display structure of each species. According to this view, the intensity of selection for small size or higher aspect ratio could be very different according to the structure of the display performed by the species. Otherwise, the existence of monogamous species with acrobatic flight displays and normal dimorphism and species with RSD and non-acrobatic displays are not incompatible with the 'display agility' hypothesis, given that in all the cases RSD has historically evolved in a clade that performed acrobatic flight displays. In this way, New Zealand snipe *Coenocorypha aucklandica* has been presented as a striking exception for the 'display agility' hypothesis (Jehl & Murray, 1986; Andersson, 1994). This species shows a noticeable reversed dimorphism and was thought not to perform any aerial display (Jehl & Murray, 1986). However, genus *Coenocorypha* is closely related to genus *Gallinago* (Lowe, 1915), composed of species with acrobatic flight displays. In this case RSD could be considered as an ancestral state character transmitted from a common ancestor of the genus *Gallinago*. Furthermore, the recent work referred to in Higgins & Davies (1996) confirmed that New Zealand snipe do in fact perform territorial flight displays with a noticeable acrobatic component, very similar to those of most *Gallinago* snipes. The understanding of other apparent exceptions to the 'display agility' hypothesis in other bird taxa presented in Andersson (1994) will need a detailed analysis of the evolutionary history of these groups, as well as a greater understanding of the components of flight performance involved in each kind of display.

The results of the comparative tests performed suggest that selection for increased agility in males in species that show acrobatic flight displays is the primary cause of the evolution of RSD in monogamous waders and determines the direction of size dimorphism. However, once the direction of dimorphism has been determined by the kind of display performed by the species, its intensity could be secondarily affected by other factors. All in all, this study has confirmed the validity of the 'display agility' hypothesis to explain the direction of size dimorphism in monogamous

waders. However, testing the performance of this hypothesis to explain on its own the magnitude of RSD is harder because of the number of factors involved (according to Jehl & Murray (1986) the sex ratio in the breeding population, the ratio of breeding males to total males and the kind of sexual display performed by the species). Finally, the lack of detailed and adequate demographic information for most species precludes an exhaustive testing of the quantitative predictions derived from the ‘display agility’ hypothesis.

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APPENDIX

Species used in the analyses. Sources: Dement'ev *et al.* (1951), Pitelka *et al.* (1974), Blake (1977), Cramp and Simmons (1983), Saether *et al.* (1983), Tomkovich and Morosov (1983), Jehl and Murray (1986), Urban *et al.* (1986), Tomkovich (1989), Jönsson and Alerstam (1990), Whitfield and Brade (1991), Marchant and Higgins (1993), Székely and Reynolds (1995) and Pierce (1997). Sexual dimorphism was expressed as the ratio of male measurements over female ones. Sexual display (Disp): Ac = Acrobatic, Na = Non-acrobatic flight display, No = No aerial display; Incubator sex (Inc): B = both, F = female, M = male; and PC (parental care category, see text).

Species	Disp	Sexual dimorphism				Breed. Latitude	Clutch size	Inc	PC
		Body mass	Wing	Bill	Tail				
<i>Thinocorus orbignyianus</i>	Na	—	1.03	1.01	1.02	25 S	4	F	1
<i>Thinocorus rumicivorus</i>	Na	—	0.99	0.98	1.02	24 S	4	F	1
<i>Gallinago gallinago</i>	Ac	0.90	1.00	0.97	1.00	58 N	4	F	2
<i>Numenius arquata</i>	Ac	0.84	0.94	0.86	0.96	60 N	4	B	5
<i>Limosa limosa</i>	Ac	0.84	0.95	0.86	0.98	50 N	4	B	3
<i>Tringa flavipes</i>	Ac	0.84	0.98	0.99	1.00	65 N	4	B	3
<i>Tringa melanoleuca</i>	Ac	0.93	0.98	0.98	1.00	59 N	4	B	3
<i>Arenaria interpres</i>	Ac	0.92	0.99	0.98	0.98	69 N	4	B	4
<i>Calidris tenuirostris</i>	Ac	0.93	0.96	0.96	0.98	65 N	4	M	6
<i>Calidris canutus</i>	Ac	0.85	0.98	0.95	1.01	72 N	4	B	5
<i>Aphriza virgata</i>	—	0.91	0.97	0.94	1.00	65 N	4	—	—
<i>Calidris maritima</i>	Ac	0.94	0.96	0.86	0.97	72 N	4	B	5
<i>Calidris ptilocnemis</i>	Ac	0.89	0.96	0.85	—	62 N	4	B	5
<i>Calidris alpina</i>	Ac	0.93	0.97	0.88	0.99	67 N	4	B	5
<i>Micropalama himantopus</i>	Ac	0.88	0.99	0.95	0.99	62 N	4	B	5
<i>Limicola falcinellus</i>	Ac	—	0.95	0.91	0.96	65 N	4	B	5
<i>Calidris subminuta</i>	Ac	0.91	0.98	0.95	0.97	65 N	4	B	5
<i>Calidris minutilla</i>	Ac	0.91	0.98	0.93	1.01	55 N	4	B	5
<i>Calidris ruficollis</i>	Ac	0.89	0.97	0.94	0.97	70 N	4	B	5
<i>Calidris mauri</i>	Ac	0.81	0.96	0.87	0.99	68 N	4	B	5
<i>Calidris pusilla</i>	Ac	0.89	0.96	0.92	0.97	64 N	4	B	5
<i>Eurynorhynchus pygmaeus</i>	Ac	0.88	0.99	0.93	—	65 N	4	B	4
<i>Calidris bardii</i>	Ac	0.91	0.97	0.94	0.97	72 N	4	B	5
<i>Vanellus senegallus</i>	—	1.00	1.00	1.00	—	0 N	4	B	3
<i>Vanellus coronatus</i>	—	—	1.01	1.03	—	10 S	3	B	3
<i>Vanellus tricolor</i>	Na	—	1.01	0.98	1.04	29 S	4	B	3
<i>Charadrius hiaticula</i>	Na	0.98	0.98	0.98	0.98	69 N	4	B	3
<i>Pluvialis apricaria</i>	Na	0.99	0.99	1.00	0.99	60 N	4	B	3
<i>Haematopus unicolor</i>	Ac	0.91	0.98	0.90	1.00	40 S	2–3	B	3
<i>Haematopus ostralegus</i>	Ac	0.95	1.00	0.89	0.99	55 N	3	B	3
<i>Himantopus himantopus</i>	Na	1.09	1.06	1.04	1.07	30 N	4	B	3
<i>Recurvirostra avosetta</i>	No	1.10	1.00	1.10	1.02	30 N	4	B	3
<i>Burhinus oedipnemus</i>	No	1.07	1.00	1.02	1.03	45 N	2	B	3
<i>Chionis alba</i>	No	1.15	1.05	1.06	1.02	50 S	3	B	3
<i>Glaucola pratincola</i>	Na	1.11	1.03	1.03	1.05	30 N	3	B	3
<i>Dromas ardeola</i>	No	—	1.00	1.02	0.99	5 N	1	F	—