Research article

The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study

OLIVER KRÜGER
Department of Zoology, University of Cambridge, Downing Street, CB2 3EJ, Cambridge, UK
(tel.: +44-1223-336610; fax: +44-1223-336676; e-mail: ok212@cam.ac.uk)

Abstract. Many hypotheses have been proposed to account for the origin and maintenance of reversed size dimorphism (RSD, females being larger than males) in hawks, falcons and owls, but no consensus has been reached. I performed comparative analyses, using both cross-taxa data and phylogenetically independent contrasts, to investigate potential correlates of reversed size dimorphism. Using a similar set of explanatory variables, covering morphology, life history and ecology, I tested whether any trait coevolved with size dimorphism in all three groups and hence provided a general explanation for the evolution of RSD. For hawks, strong correlates were found in the foraging-variable complex, so RSD might have evolved in species hunting large and agile prey. This is consistent with the intersexual-competition hypothesis (sexes have evolved different sizes to lessen intersexual competition for food), but especially the small-male hypothesis (males have evolved to be smaller to be more efficient foragers). Evolutionary pathway analyses suggest that RSD evolved most likely as a precursor of changes in hunting strategy but as a consequence of high reproduction. The falcons showed a similar pattern: species with strong RSD hunted larger and more agile prey. The evolutionary pathway analysis supported the idea that RSD evolved before the specialisation on more agile and/or larger prey. Finally for owls, the results showed clear parallels. RSD increased with prey size, consistent with the small-male hypothesis. Evolutionary pathway analysis suggests that RSD in owls has most likely evolved before specialisation on large prey, so a small and more agile male might be advantageous even when hunting small prey. These results suggest that RSD in hawks, falcons and owls evolved due to natural-selection pressures rather than sexual-selection pressures.

Key words: intersexual-competition hypothesis, natural selection, reversed size dimorphism, sexual selection, small-male hypothesis

Introduction

In most animal species, males and females differ in size, sometimes substantially (Webster, 1992; Fairbairn, 1997; Colwell, 2000; Székely *et al.*, 2000). The evolutionary and ecological significance of intersexual size differences has attracted attention since Darwin (1871). In most avian and mammalian lineages, male–male competition for females has led to an increase in male size due to sexual selection, and hence males are larger than females (Darwin, 1871;

Andersson, 1994; Colwell, 2000). However, in some families of birds and bats, reversed size dimorphism (RSD) exists; females are the larger sex (Ralls, 1976; Myers, 1978; Mueller, 1990; Owens and Hartley, 1998). RSD in birds is mainly found in four taxa (Paton *et al.*, 1994): the hawks and eagles (Accipitridae), the falcons (Falconidae), the owls (Strigiformes) and the waders (Charadriiformes). The question is which changes in morphology, life history and ecology have gone in hand with the evolution of RSD within these four groups: what happened within these four groups that sets them apart from other taxa, allowing RSD to have evolved.

Well in excess of 20 hypotheses, which can be divided into three main groups, have been proposed to explain the evolution and maintenance of RSD in these four bird groups (Andersson and Norberg, 1981; Cade, 1982; Mueller and Meyer, 1985; Jehl and Murray, 1986). Ecological hypotheses stress the selective advantage of size dimorphism in niche partitioning, as it lessens intersexual competition (Reynolds, 1972; Newton, 1979; Temeles, 1985). A weakness of these hypotheses is that they do not predict which sex should be larger. Role-differentiation hypotheses (Selander, 1972; Snyder and Wiley, 1976; Schantz and Nilsson, 1981; Ydenberg and Forbes, 1991) suggest that either females have become larger to form and/or protect a larger egg or to increase incubation efficiency (large-female hypothesis), or males have become smaller for more efficient foraging or territory defence (small-male hypothesis), see Massemin *et al.* (2000) for a detailed comparison. Behavioural hypotheses suggest that female size has increased to dominate the male and hence aid maintenance of the pair bond and to increase food provisioning by the male through this female dominance (Amadon, 1975; Mueller, 1986), or because females compete for males (Olsen and Olsen, 1987; Olsen and Cockburn, 1993), or because males are selected to become smaller and more agile to perform acrobatic aerial displays (Andersson and Norberg, 1981; Hakkarainen *et al.*, 1996). Table 1 lists the main hypotheses with their reasoning and also specifies which potential correlate variables can be expected to be important if a particular hypothesis is likely to explain the evolution of RSD. However, the ultimate requirement is to establish the relative importance of natural and sexual selection for the evolution and maintenance of RSD (Mueller, 1990; Kissner *et al.*, 2003).

Because it is extremely difficult to test most hypotheses in the field (Andersson and Norberg, 1981), the comparative approach has generally been applied (Newton, 1979; Mueller and Meyer, 1985; Jehl and Murray, 1986; Owens and Hartley, 1998). However, several recent studies focussed on one species and used variation in RSD between breeding pairs to test the different role-differentiation hypotheses (Hakkarainen and Korpimäki, 1991, 1993, 1995; Catry *et al.*, 1999; Tornberg *et al.* 1999; Massemin *et al.*, 2000; Phillips *et al.*, 2002).

Table 1. The three main different hypotheses aiming to explain the evolution of RSD, with the predicted sex which should evolve a different size, the reasoning behind the selective advantage of RSD and expected main correlates from the candidate variable list of Table 2

Hypothesis	Evolutionary outcome	Selection pressure	Associated with
Ecological	sexes diverge in size	Reduced intersexual competition	Larger niche breadth
			Less prey specialisation
			Less habitat productivity
			Higher population density
Role-differentiation	♀ becomes larger than ♂	Large egg formation, better incubation	Larger egg size
			Larger residual egg size
			Larger clutch size
			Shorter incubation time
	♂ becomes smaller than ♀	Increased male agility	More demanding hunting method
			More prey specialisation
			Larger prey size
			Higher reproduction rate
Behavioural	♀ becomes larger than ♂	Female dominance over male	Higher reproduction rate
	♀ becomes larger than ♂	Female competition for male	More plumage dimorphism
			Changes with breeding system
	♂ becomes smaller than ♀	Male flight display selected for	More acrobatic display
			Changes with breeding system

Debate about the relative importance of various hypotheses explaining RSD has partly arisen because most studies focus either on birds of prey (Newton, 1979; Cade, 1982) or on waders (Jehl and Murray, 1986; Figuerola, 1999; Lindenfors *et al.*, 2003). Based on the taxon-specific results, hypotheses have been formulated and subsequently criticised because they lack generality

(Mueller, 1990; Jehl and Murray, 1986; Mueller and Meyer, 1985). To test effectively any hypothesis for generality requires both a large data set and the measurement of many variables in at least two groups. Although hawks, falcons and owls differ in their breeding systems, life history and ecology, variables were chosen which could be measured with reasonable accuracy and which were comparable across the three bird taxa. While modern comparative analyses have dealt with the waders (Figuerola, 1999; Székely *et al.*, 2000; Lindenfors *et al.*, 2003), such an analysis is surprisingly lacking for the three most diverse predatory bird groups: hawks, falcons and owls.

It is now widely accepted that cross-taxa analyses might be confounded by effects of phylogeny (Harvey and Pagel, 1991). For example, many authors have stressed the correlation between prey group and RSD in hawks (Reynolds, 1972; Newton, 1979; Sigurjónsdóttir, 1981). However, the most species-rich genus *Accipiter*, comprising almost 25% of all hawk species, might produce most of this correlation, with most species hunting birds and mammals, and also exhibiting strong RSD (Ferguson-Lees and Christie, 2001).

The aims in this paper were hence 3-fold. First, a comparative analysis using cross taxa data, as well as controlling for phylogeny by calculating independent contrasts (Felsenstein, 1985; Harvey and Pagel, 1991), was completed for hawks, falcons and owls to establish important correlates of RSD. In a second step, the results were compared to test whether one underlying hypothesis is likely to explain the evolution and maintenance of RSD or whether a different explanation is required for hawks, falcons and owls. Thirdly, I tested whether the important correlates of changes in size dimorphism were most likely to be either causes or consequences, by establishing the most likely evolutionary pathway (Pagel, 1999; Krüger and Davies, 2002).

Materials and methods

I collected data on the 237 species in the family Accipitridae (hawks), on the 61 species in the family Falconidae (falcons) and on the 212 species in the order Strigiformes (owls) from the literature (mainly Thiollay, 1994; König *et al.*, 1999; Krüger, 2000; Ferguson-Lees and Christie, 2001). The dependent variable, RSD, was measured as the wing length of males (mm) divided by the wing length of females (mm), and this ratio was subsequently cubed to reflect differences in bulk as well (Ferguson-Lees and Christie, 2001, p. 35). Wing-length data were available for more species (not for every species, hence differences in sample size in the Results section) than body-mass data, and the cubed index has been used as an estimate of differences in both bulk and flight performance, and is commonly used (Ferguson-Lees and Christie, 2001). Moreover, body mass fluctuates greatly between seasons in hawks and owls, which would

introduce extra noise into the data set (Newton, 1979). Wing-length data are more reliable in this respect. Ranta *et al.* (1994) have pointed out that ratios do not have the same statistical properties as the original data, which can lead to erroneous conclusions. They state that a ratio should only be used if the regression of the female trait against the male trait is linear and passes through the origin. I tested this for the wing-length data, and as can be seen from Figure 1, the relationship is linear in hawks but all three groups showed the same qualitative pattern (no non-linear term in any regression model type was significant) and the reduced major axis slopes were not statistically different from one (McArdle, 1988, hawks: $t = 1.131$, $df = 156$, $p = 0.210$, falcons: $t = 1.835$, $df = 42$, $p = 0.076$ owls: $t = 1.766$, $df = 39$, $p = 0.085$). Hence, using wing-length ratio as the dependent variable seems statistically justified.

In the analyses, 26 predictor variables were included for hawks and falcons and 22 for owls (Table 2). These variables were selected because they are expected to be important correlates if the various hypotheses explain the evolution of RSD (Table 1) or because they are needed to control for allometric or biogeographical effects. The difference between the two groups in variable number was because some variables could not be retrieved reliably for owls. The large number of predictor variables allows the control of confounding variables and the assessment of the relative importance of factor complexes, such as morphology, life history and ecology. Because half and quarter values were sometimes used in the categorical variables, they were treated as continuous in the analyses.

The variable sexual plumage dimorphism was adopted from Krüger and Davies (2002) and was scored as follows: $0 =$ no difference, $1 =$ slight difference (eye colour or eye ring), $2 =$ difference (less than 25% of the plumage), $3 =$ marked difference (more than 25% of the plumage), $4 =$ different plumage. A world-population estimate for each hawk and falcon species was obtained
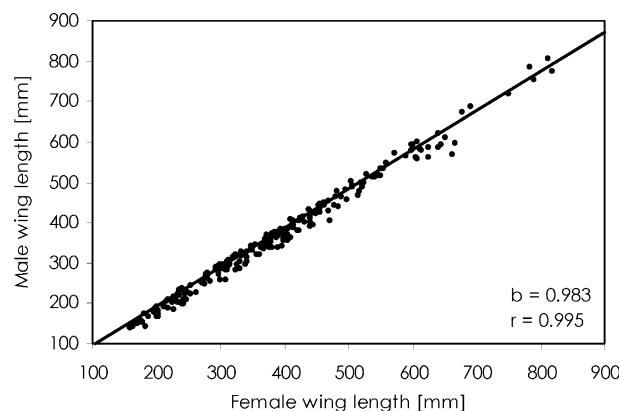

Figure 1. Scatterplot of female wing length against male wing length for hawks.

Table 2. Explanatory variables included in the analyses and their description

Variable	Description	Hawks	Falcons	Owls
Body mass	Log body mass (g)	+	+	+
Body size	Body size from tip of bill to tip of tail (cm)	+	+	+
Wingspan	Wingspan (cm)	+	+	
Wing length	Wing length (cm)	+	+	+
Tail length	Tail length (cm)	+	+	
Sex plum. dimorphism	Scored from 0 (no difference) to 4 (entirely different plumage), after Krüger and Davies (2002)	+	+	+
Plum. polymorphism	Number of described plumage morphs	+	+	+
Population density	Mean number of breeding pairs/100 km^2 across studies	+	+	+
Population size	Log world population estimate in breeding pairs	+	+	
Breeding system	-1 = polygyny, 0 = monogamy, 1 = polyandry	+	+	+
Display behaviour	1 = ground display, 2 = aerial non-acrobatic display, 3 = aerial acrobatic display, 4 = very acrobatic display	+	+	
Egg volume	Log estimated egg volume (ml)	+	+	+
Clutch size	Mean clutch size	+	+	+
Incubation time	Mean incubation time (days)	+	+	+
Fledging time	Mean fledging time (days)	+	+	+
Reproduction rate	Mean number of chicks fledged/pair and year	+	+	+
Prey size	1 = fruits, 2 = insects, 3 = snails, 4 = frogs, 5 = lizards, 6 = snakes, 7 = fish, 8 = rodents, 9 = birds, 10 = small carrion, 11 = mammals, 12 = large carrion	+	+	+
Prey specialisation	Scored from 1 (opportunist) to 4 (extreme specialist), after Krüger (2000)	+	+	+
Hunting method	Scored from 1 (only searching) to 4 (attacks on agile prey with defence potential), after Krüger (2000)	+	+	+
Habitat preference	1 = tropical forest, 2 = subtropical & temperate forest, 3 = woodland, 4 = freshwater habitats, 5 = coastline, 6 = marsh, 7 = savannah, 8 = grassland, 9 = mountain, 10 = semi-desert	+	+	+
Niche breadth	Number of habitats a species breeds in	+	+	+
Habitat productivity	Productivity in g carbon m^{-2} per year (Reichle 1970)	+	+	+
Breeding altitude	Median breeding altitude above sea-level (m)	+	+	+
Breeding latitude	Median breeding latitude (°)	+	+	+
Migration pattern	Scored from 0–4 (Krüger and Davies 2002)	+	+	+
Range size	Log global breeding range size (km^2)	+	+	+

from Ferguson-Lees and Christie (2001) and, although such estimates become increasingly crude with increasing abundance, they provide an estimate of present population size. Except for cases where a population change has resulted from anthropogenic causes, the population estimate also roughly

reflects the likely population size in the past. Egg volumes were estimated from egg length and breadth measurements in Schönwetter (1967–1992) and the approximation for egg volume provided by Hoyt (1979). Residual egg volume (corrected for the allometric relationship with body mass) was also included as a variable in the analyses, because several authors have suggested this to be an important correlate of RSD (Pleasants and Pleasants, 1988; Weatherhead and Teather, 1994). I also calculated residual clutch volume (egg volume times clutch size, subsequently corrected for body mass) but the results did not change qualitatively and hence only the relationship with residual egg volume is reported here. In most cases, prey-size categories were separated by approximately an order of magnitude in mass. The variable prey size could also be interpreted as a crude estimate of prey type abundance. The variable prey specialisation was adopted from Krüger (2000) and scored as 1 = generalist, 2 = opportunist, 3 = specialist, 4 = extreme specialist. The variable 'hunting method' was included to reflect the energetic cost of hunting and the aerial-skill level needed (following Krüger, 2000) and was scored as follows: 1 = no hunting skills necessary, only searching, 2 = searching and handling/killing necessary, 3 = attacks on prey that has low defence or escape potential, 4 = attacks on prey that has high defence or escape potential. The habitat-preference variable was ranked from closed canopy habitat to increasingly more open and less productive habitat, hence there is some overlap with the habitat-productivity variable. The variable migration pattern was again adopted from Krüger and Davies (2002) and scored as 0 = resident, 1 = rare migrant (vacates less than 25% of breeding area), 2 = partial migrant (vacates 25–75% of breeding area), 3 = migrant (vacates more than 75% of breeding area), 4 = long distance migrant (vacates 100% of breeding area and migrates commonly more than 5000 km). Global breeding-range size was calculated for hawks and falcons from information in Ferguson-Lees and Christie (2001) and for owls by overlaying the distribution maps with world country maps and calculating the breeding range size from this comparison with known country geographic area sizes. All other measured variables are self-explanatory or have been described in more detail elsewhere (Table 2; Fowlie and Krüger, 2003).

I performed both a cross-taxa analysis, treating each taxon as an independent data point, and calculated phylogenetically independent contrasts, using the method of Felsenstein (1985) as implemented in CAIC (Purvis and Rambaut, 1995). I included a cross-taxa analysis because, although formerly believed to yield erroneous conclusions (Harvey and Pagel, 1991), there is recent evidence that they can be as statistically valid and as biologically informative as independent contrasts (Price, 1997; Harvey and Rambaut, 2000). The comparative analyses for hawks were based on two separate phylogenies: the osteological phylogeny of genera by Holdaway (1994) and the

molecular phylogeny of species by Wink and Sauer-Gürth (2000). The reason for performing two independent analyses on the hawks, using two different phylogenies, was to test the robustness of the qualitative results, because it is known that comparative results are sensitive to the phylogenies used (Harvey and Pagel, 1991). I used the molecular phylogeny of falcons in Wink and Sauer-Gürth (2000) and for owls, I used a molecular phylogeny of species provided by Wink and Heidrich (1999). Neither of the four phylogenies was combined with any other phylogenetic information and branch lengths were set to unity. All four of these phylogenies are the most comprehensive available for the groups and agree well with the well-established phylogeny of Sibley and Ahlquist (1990).

I developed multivariate stepwise forward regression models in SPSS for all three taxa. Species with missing data were excluded from the analyses, which reduced sample size in the cross-taxa analyses. However, results remained qualitatively similar if missing data were replaced by means. The models for independent contrasts did not include an intercept, as recommended by Harvey and Pagel (1991). To address the problem of multicollinearity, I looked at tolerance levels and only included variables above 0.1 tolerance, as recommended by Hair *et al.* (1995). Models were only considered valid if residuals were distributed normally (James and McCulloch, 1990). To test for allometry in RSD, reduced major axis regressions were used (McArdle, 1988), which are more appropriate in cases where there is random error in both variables and the choice of predictor variable is arbitrary.

To test whether the most important predictor variables of changes in RSD were more likely to be causes or consequences, I used Pagel's discrete variable method (Pagel, 1994, 1999). This method tests the temporal ordering and direction of evolutionary change and establishes the most probable evolutionary pathways between two traits (Rolland *et al.*, 1998; Cezilly *et al.*, 2000). This allows disentangling of the most likely cause and effect of a correlation and hence can take comparative studies beyond the purely correlational stage (van Noordwijk, 2002). Because variables need to be dichotomous for this method, I used the mean of continuous data as a threshold. As the method can only use two variables at a time, controlling for confounding variables is not possible. Pagel's method uses likelihood ratio (LR) tests to determine whether two traits have evolved independently or dependently along a phylogeny. After establishing that two traits show correlated evolution, it allows an estimate of the significance of each of the eight transitions possible between two dichotomous variables. The presumed ancestral state was inferred from a comparison with the most likely sister order, storks (Ciconiiformes) for the hawks and falcons, and nightjars (Caprimulgiformes) for the owls (Thiollay, 1994; König *et al.*, 1999).

Results

Distribution of size dimorphism in the three groups

Across hawk species, RSD (measured as cubed wing length ratios) ranged from 0.53 in the Madagascar sparrowhawk (*Accipiter madagascariensis*) to 1.00 in the Himalayan griffon (*Gyps himalayensis*); (mean $\pm$ SE $= 0.818 \pm 0.007$, $n = 232$). The distribution was normal but slightly skewed towards smaller relative male size (Fig. 2, top panel). Across falcons, RSD ranged from 0.61 in the bat falcon (*Falco rufigularis*) to 0.99 in the black caracara (*Daptrius ater*); (mean $\pm$ SE $= 0.850 \pm 0.013$, $n = 61$). The distribution was similar to hawks with a slight skew towards smaller relative male size (Fig. 2, middle panel). Across owls, relative male size ranged between 0.68 in the greater sooty owl (*Tyto tenebricosa*) and 1.18 in the rufous owl (*Ninox rufa*), mean $\pm$ SE $= 0.903 \pm 0.008$, $n = 100$). The distribution was normal without any signs of skew (Fig. 2, bottom panel).

Hawks

Across hawk species, the best regression model was highly significant ($F_{3,104} = 29.592$, $p < 0.0001$), explained 46.8% of the variation in RSD and included three predictor variables (Table 3). Prey size and hunting method were negatively correlated with RSD, while wing length showed a positive correlation. Across hawk genera, only hunting method was a significant predictor (Table 3). It alone produced a highly significant model ($F_{1,54} = 38.606$, $p < 0.001$) and explained 41.7% of the variation in RSD. Again, there was a negative correlation between hunting method and RSD, indicating that species hunting large, agile and scattered prey with a high defence potential had particularly small males.

Independent contrasts analysis produced no evidence for allometry in size dimorphism in hawks (reduced major axis slope $= 0.990$, 95% confidence interval $= 0.939$–1.044). The best multiple regression model for hawk species contrasts included only one predictor variable: hunting method (Table 4). The model was highly significant ($F_{1,52} = 20.623$, $p < 0.0001$) and explained 28.4% of the variation in RSD. The multiple regression model for hawk genera contrasts included three predictor variables (Table 4). RSD was positively correlated with migration, while it was negatively correlated with reproduction rate and hunting method. The model was highly significant ($F_{3,37} = 6.213$, $p = 0.002$) and explained 33.5% of the variation in RSD.

Falcons

Across falcon species, the best regression model was highly significant ($F_{3,32} = 32.986$, $p < 0.001$), and explained 75.6% of the variation in RSD
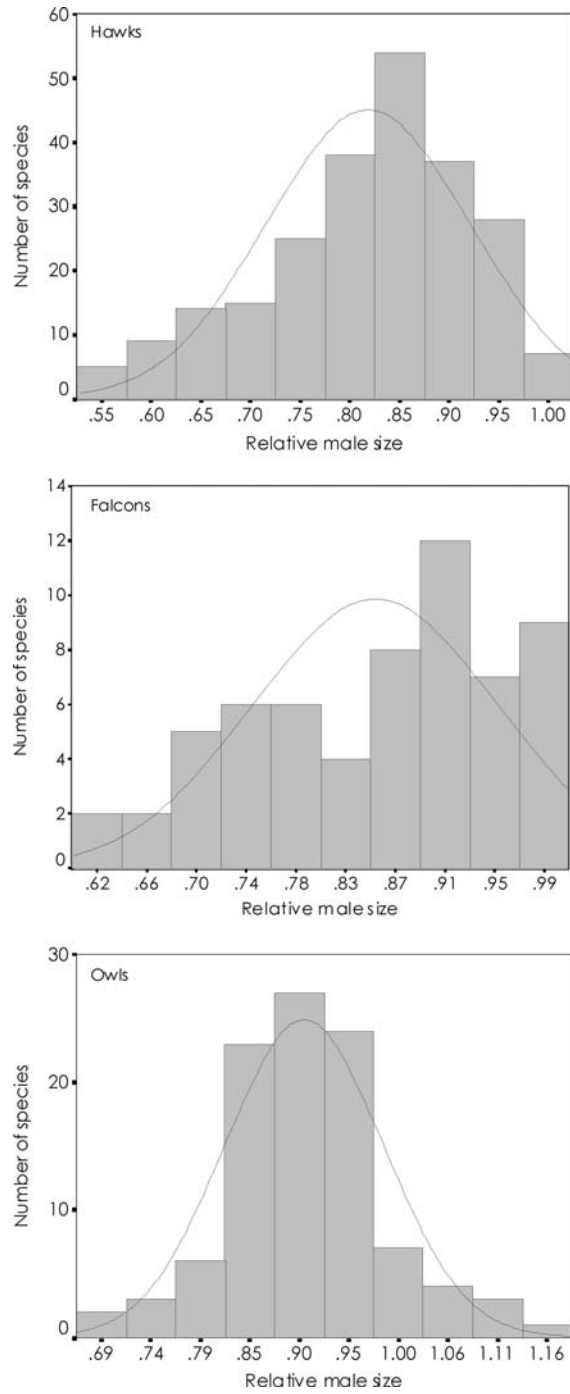
Figure 2. Histograms of the distribution of RSD in hawks, falcons and owls. The lines show the normal distribution.

Table 3. Multiple regression models of RSD across taxa for hawk species (top) and genera (bottom)

Variable	β	SE	t	p	R^2	Collinearity
Cross species (n = 108)						
Constant	0.856	0.034	25.430	0.001		
Hunting method	−0.048	0.012	3.862	0.001	0.236	0.845
Wing length	0.004	0.001	6.630	0.001	0.392	0.666
Prey size	−0.015	0.004	3.800	0.001	0.468	0.661
Cross genera (n = 56)						
Constant	0.972	0.020	48.026	0.001		
Hunting method	−0.068	0.011	6.213	0.001	0.417	1.000

The SE of the estimates are 0.076 and 0.063, respectively and residuals were normally distributed.

and included three predictor variables (Table 5). Hunting method and clutch size were negatively correlated with RSD whereas sexual plumage dimorphism was positively correlated with RSD, indicating that species with smaller males hunted more agile, and/or larger and rarer prey and had a higher clutch size but showed smaller plumage differences between the sexes.

The contrast analysis produced no evidence for allometry in size dimorphism in owls either (reduced major axis slope = 0.963, 95% confidence interval = 0.894–1.037). The best multiple regression model for falcon contrasts included three predictor variables (Table 5), was highly significant ($F_{3,18} = 21.390$, $p < 0.001$) and explained 78.1% of the variation in RSD. Like in the cross species analysis, RSD was negatively correlated with hunting method and positively with sexual plumage dimorphism. In addition, reproduction rate was negatively correlated with RSD.

Table 4. Multiple regression models for RSD contrasts of hawk species (top) and genera (bottom)

Variable	β	SE	t	p	R^2	Collinearity
Species contrasts (n = 53)						
Hunting method	−0.065	0.014	4.541	0.001	0.284	1.000
Genera contrasts (n = 40)						
Reproduction rate	−0.087	0.027	3.169	0.003	0.127	0.969
Migration pattern	0.027	0.010	2.679	0.011	0.250	0.971
Hunting method	−0.035	0.016	2.175	0.036	0.335	0.997

The SE of the estimates are 0.021 and 0.027, respectively and residuals were normally distributed. The much smaller number of contrasts compared to the cross-taxa analyses in Table 3 was caused by the phylogenies, which included only 54 species and 41 genera of hawks, respectively.

Owls

Across owl species, the best regression model was significant ($F_{1,57} = 6.649$, $p = 0.013$), and explained 10.4% of the variation in RSD and included one predictor variable (Table 6). As in the species model for hawks, RSD was large in species hunting agile and/or large and rare prey with a high defence potential.

The contrast analysis produced no evidence for allometry in size dimorphism in owls either (reduced major axis slope = 1.010, 95% confidence interval = 0.972–1.048). The regression model, which was highly significant ($F_{1,56} = 8.502$, $p = 0.005$), explained 13.2% of the variation in RSD and included one predictor variable (Table 6). RSD was negatively correlated with prey size. Prey size was also a significant predictor variable in the hawk cross species model.

Evolutionary pathways

I selected the most important variable explaining variation in RSD from each of the four contrast analyses which were hunting method for the hawk species phylogeny, reproduction rate for the hawk genera phylogeny, hunting method for the falcon species phylogeny and prey size for the owl species phylogeny to be analysed using Pagel's method.

Focussing on the hawk species phylogeny (Figure 3a), there was evidence of correlated evolution between size dimorphism and hunting method (independent model = −39.901, dependent model = −26.889, likelihood ratio = 26.024, $df = 4$, $p < 0.001$). Significant evolutionary pathways were found both ways between the states 'small male & hard hunt' and 'large male & hard hunt' (q_{24}: likelihood ratio = 23.380, $df = 1$, $p < 0.001$ and q_{42}: likelihood ratio = 6.014, $df = 1$, $p < 0.05$). In addition, there was a trend for the transition from 'small male & easy hunt' towards 'small male & hard hunt' (q_{12}: likelihood

Table 5. Multiple regression models for RSD across falcon species (top) and using contrasts (bottom)

Variable	β	SE	t	p	R^2	Collinearity
Cross species ($n = 36$)						
Constant	1.164	0.045	25.868	0.001		
Hunting method	−0.082	0.013	6.449	0.001	0.619	0.829
Plumage dimorphism	0.035	0.009	3.971	0.001	0.670	0.674
Clutch size	−0.047	0.014	3.343	0.002	0.756	0.702
Species contrasts ($n = 22$)						
Hunting method	−0.071	0.016	4.522	0.001	0.546	0.852
Plumage dimorphism	0.021	0.006	3.493	0.003	0.675	0.935
Reproduction rate	−0.045	0.015	2.956	0.008	0.781	0.904

The SE of the estimates are 0.052 and 0.018, respectively and residuals were normally distributed.

Table 6. Multiple regression models for RSD across owl species (top) and using contrasts (bottom)

Variable	β	SE	t	p	R^2	Collinearity
Cross species ($n = 58$)						
Constant	0.985	0.032	30.427	0.001		
Hunting method	−0.046	0.018	2.578	0.013	0.104	1.000
Species contrasts ($n = 57$)						
Prey size	−0.014	0.005	2.916	0.005	0.132	1.000

The SE of the estimates are 0.060 and 0.028, respectively and residuals were normally distributed.

ratio $= 3.398$, $df = 1$, $p < 0.1$). Unfortunately no significant pathway was found linking the presumed ancestral state of 'large male & easy hunt' to other states, hence it is difficult to reconstruct the most likely temporal ordering of evolutionary events.

Focussing on the hawk-genera phylogeny, there was evidence for correlated evolution between size dimorphism and reproduction rate (Figure 3b, independent model $= -50.101$, dependent model $= -42.162$, likelihood ratio $= 15.878$, $df = 4$, $p < 0.005$). From the presumed ancestral state 'large male & low reproduction', there were significant pathways both ways to the state 'large male & high reproduction' (q_{34}: likelihood ratio $= 11.542$, $df = 1$, $p < 0.001$ and q_{43}: likelihood ratio $= 12.144$, $df = 1$, $p < 0.001$). Significant pathways also linked this state to the state displayed by most extant hawk species, 'small male & high reproduction' (q_{42}: likelihood ratio $= 9.412$, $df = 1$, $p < 0.005$ and q_{24}: likelihood ratio $= 9.456$, $df = 1$, $p < 0.005$). This seems to indicate that, given the presumed ancestral state, a change in reproduction rate preceded a change in relative male size.

With regard to falcons, there was evidence for correlated evolution between size dimorphism and hunting method (Figure 3c, independent model $= -19.902$, dependent model $= -15.123$, likelihood ratio $= 9.558$, $df = 4$, $p < 0.05$). From the presumed ancestral state 'large male & easy hunt', there was a significant pathway to the state 'small male & easy hunt' (q_{31}: likelihood ratio $= 7.616$, $df = 1$, $p < 0.01$). From this state, there was a trend linking this state to the state 'small male & hard hunt' (q_{12}: likelihood ratio $= 2.770$, $df = 1$, $p < 0.1$) which was in turn linked to the state 'large male & hard hunt' by a trend (q_{24}: likelihood ratio $= 3.050$, $df = 1$, $p < 0.1$). These pathways seem to indicate that changes in relative male size preceded changes in hunting method, i.e. a smaller male was selected for before specialisation on larger and more agile prey evolved.

With regard to owls, there was evidence for correlated evolution between size dimorphism and prey size (Figure 3d, independent model $= -74.257$, dependent model $= -68.131$, likelihood ratio $= 12.252$, $df = 4$, $p < 0.02$). From the presumed ancestral state 'large male & small prey', there was a significant pathway to the
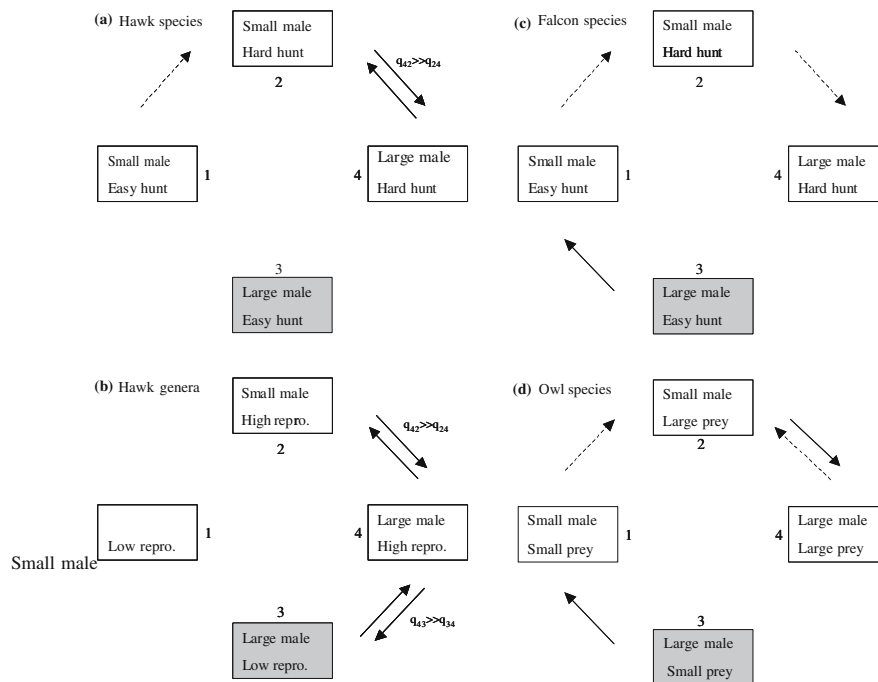
Figure 3. Flow diagram depicting the most probable evolutionary pathways between RSD and (a) hunting method for the hawk species phylogeny, (b) reproduction rate for the hawk genera phylogeny, (c) hunting method for the falcon phylogeny and (d) prey size for the owl species phylogeny. In each figure part, the presumed ancestral state is shaded in grey. Solid arrows represent significant evolutionary pathways ($p < 0.05$) and dashed arrows represent trends ($p < 0.1$). A comparison of transition rates (q) is provided when both pathways were significant, with subscripts indicating the transition direction.

state 'small male & small prey' (q_{31}: likelihood ratio $= 6.126$, $df = 1$, $p < 0.05$). From this state, there was a trend linking this state to the state 'small male & large prey' (q_{12}: likelihood ratio $= 3.224$, $df = 1$, $p < 0.1$). In addition, there was a significant pathway linking this state to the state 'large male & large prey' and a vice versa trend (q_{24}: likelihood ratio $= 4.470$, $df = 1$, $p < 0.05$ and q_{42}: likelihood ratio $= 3.708$, $df = 1$, $p < 0.1$). These pathways seem to indicate that changes in relative male size preceded changes in prey size, because the linkage from the presumed ancestral state to the one displayed by most extant species (small male and large prey) was significant only via changes in size dimorphism preceding changes in prey size and not vice versa.

Discussion

By considering the three main predatory bird groups, I was able to test the generality of the various hypotheses proposed for the origin and maintenance

of RSD. During the radiation of the three bird taxa, RSD seems to have been maintained by similar selection pressures.

What do these results mean for the variety of hypotheses proposed to account for the origin and maintenance of RSD? One set of hypotheses not supported by my analysis proposes females are larger because of the burden of egg formation, laying and incubation (Selander, 1972; Cade, 1982; Pleasants and Pleasants, 1988; Weatherhead and Teather, 1994). Neither residual egg volume, nor residual clutch volume entered any model explaining RSD, both using cross-taxa data and contrasts. I would argue, therefore, that there is little support for the general importance of egg size in the evolution of RSD.

Among the hypotheses in the sexual-selection complex, my results do not support the hypothesis that the larger females compete for smaller males (Olsen and Olsen, 1984, 1987; Olsen and Cockburn, 1993). Although female hawks, falcons and owls are larger than their male counterparts, we see more brightly coloured plumage in males and this is commonly associated with female choice and male-male competition for access to females (Barraclough *et al.*, 1995; Parker and Partridge, 1998). The general importance of sexual selection is doubtful, because only in the falcons did any of the variables (sexual plumage dimorphism) enter a regression model explaining size dimorphism. There was also no support for the hypothesis that males were sexually selected to become smaller in order to perform acrobatic flight displays, because this variable also did not enter any of the regression models.

There seems to be some support for the intersexual-competition hypothesis but general support for the small-male hypothesis by which the sexes either reduce competition for prey as the driving force behind the evolution of RSD, as proposed by Reynolds (1972), Newton (1979) and Sigurjónsdóttir (1981), or that males have become smaller in order to forage more effectively and on more agile and/or larger and rarer prey (Ydenberg and Forbes, 1991; Tornberg *et al.*, 1999). All three groups seem to conform to the predictions made by this hypothesis. These results also agree with those obtained in field studies on European kestrels (*Falcon tinnunculus*), Tengmalm's owls (*Aegolius funereus*) and Goshawks (*Accipiter gentilis*) where the small-male hypothesis was also the most likely hypothesis (Hakkarainen and Korpimäki, 1995; Tornberg *et al.*, 1999; Massemin *et al.*, 2000).

For hawks, strong correlates were found within the foraging-variable complex. Large RSD seems to have co-evolved with feeding on agile and/or larger and rarer prey species. This has been found before by several authors, who hypothesised that either intersexual competition for food or selection on males to become more efficient foragers might be the underlying cause (Balgooyen, 1976; Newton, 1979; Anderson and Norberg, 1981; Sigurjónsdóttir, 1981; Ydenberg and Forbes, 1991). Evidence for how quick an evolutionary response in male size can be has been provided by Tornberg *et al.* (1999) who

showed that male goshawks decreased significantly in body size within 40 years as a response to a change in diet towards more agile, smaller prey. For hawks, the evolutionary pathway analysis did not resolve whether a change towards hunting more agile prey preceded the evolution of RSD or was a consequence of it. Hence, RSD might either be a consequence of specialisation on more agile and/or larger, less abundant prey species, or a cause.

Interestingly, another predictor of RSD for hawk genera contrasts was reproduction rate. The evolutionary pathway analysis suggests that greater RSD was selected for to sustain an enhanced reproduction rate, most likely via more efficient food provisioning to the young, again supporting the small-male hypothesis (Storer, 1966; Reynolds, 1972). RSD seems to have evolved as a consequence of a change in the life-history strategy and not vice versa.

The logic behind the foraging-efficiency hypothesis has been seriously challenged by Mueller (1990), who argued that selection for size dimorphism can only act on sex-linked or sex-limited genes. However, this ignores the possibility of a counteracting selection pressure acting on females only (Arak, 1988; Ydenberg and Forbes, 1991; Massemin et al., 2000). Indeed the evolution of RSD might be best understood as selection pressures acting differently on the two sexes (Arak, 1988; Tornberg et al., 1999). As a consequence, there might be a selection pressure to reduce body size in both sexes, but females might be constrained, possibly because of their necessity to form, protect and incubate a large egg (Selander, 1972; Walter, 1979; Cade, 1982). However, this particular hypothesis was not supported in my analyses because neither residual egg volume nor residual clutch volume did enter any model explaining RSD in either hawks, falcons or owls.

For the falcons, the results were quite similar. The strongest correlate with RSD was hunting method, which had been an important predictor for hawks as well. Interestingly, the evolutionary pathway analysis suggested strongly that the evolution of RSD preceded the specialisation on more agile and/or larger and rarer prey. Hence RSD might have evolved for more efficient foraging (another important correlate was reproduction rate), fitting the small-male hypothesis, which was followed by specialisation on more agile and/or larger and rarer prey.

For owls, the results were again very similar. This tends to support the idea that the predatory habit per se is an important trait maintaining RSD (Newton, 1979; Ferguson-Lees and Christie, 2001). Norberg (1987) stated that any hypothesis explaining RSD should equally apply to hawks and owls, and my findings indicate that the most likely candidate is the small-male hypothesis. In contrast to the hawk evolutionary pathway analyses but in line with the falcons, the most likely temporal ordering of events for owls seems to be that a change in RSD preceded the change in prey size (Figure 3d). Hence, RSD seems to have enabled the specialisation on larger prey. This means that a small

male or a large female was initially selected for, and this preceded specialisation on larger prey. However, Hakkarainen and Korpimäki (1995) showed in their study on Tengmalm's owl how variable selection pressure on male size can be over time, so any interpretation of the pathway analyses must necessarily remain cautious. Which sex evolved a different size and why remains speculative but the importance of prey size as a correlate of changes in size dimorphism once again points towards the intersexual-competition hypothesis and/ or the small-male hypothesis as one important explanation. The importance of male foraging ability is particularly great in hawks, falcons and owls, because the male provides food for the incubating female and is also the sole hunter during the first half of the chick-raising period in the majority of species (Thiollay, 1994; König et al., 1999), hence his foraging ability greatly influences reproductive success and fitness of both sexes.

In waders, the importance of sexual-selection pressures seems to be paramount (Székely et al., 2000; Lindenfors et al., 2003). Sexual selection has also been proposed as a driving force for skuas and jaegers Stercorariidae (Catry et al., 1999; but see Phillips et al., 2002 for contradictory results). I would tentatively argue that the small-male hypothesis is the most likely general explanation for the evolution of reversed size dimorphism in hawks, falcons and owls.

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