Selection on females can create 'larger males'

Jordan Karubian[1] **and John P. Swaddle**[2]

[1]*Department of Ecology and Evolution, University of Chicago, 1101 East 57th Street, Chicago, IL 60637, USA*
[2]*Sapient Corporation, 213 West Institute Place, Suite 509, Chicago, IL 60610, USA*

In many bird and mammal species, males are significantly larger than females. The prevailing explanation for larger-sized males is that sexual selection drives increased male size. In addition, researchers commonly assume that the extent of dimorphism indicates the strength of selection for increased size in males. Here, through reconstruction of ancestral morphology for males and females of one large avian clade we present data that contradict this assumption and illustrate that selection for decreased female size explains 'male-biased' dimorphism *ca.* 50% of the time. Our findings are also inconsistent with ecological niche partitioning between the sexes and increased breeding benefits from reduced female size as general explanations for the evolution of size dimorphism within the clade. We conclude that it is incorrect to assume sexual dimorphism results from a single selective factor, such as directional sexual selection on increased male size. Rather, we suggest that the selective forces leading to sexual dimorphism may vary between species and should be tested on a case-by-case basis using a phylogenetic approach.

Keywords: Aves; niche-partitioning hypothesis; sexual dimorphism; sexual selection

1. INTRODUCTION

Darwin first suggested that male-biased sexual size dimorphism was the result of sexual selection driving an increase in male body size (Darwin 1871). In birds, sexual selection hypotheses have received substantial support (Jehl & Murray 1986; Andersson 1994), and although a number of competing hypotheses exist (Jehl & Murray 1986; Andersson 1994) 'sexual selection has received virtually universal acceptance as an explanation for normal (male biased) sexual dimorphism' (Mueller 1990). A recent review, for example, concludes that 'sexual size dimorphism is the result of sexual selection . . . the initial morphological division between the sexes cannot arise from ecological selection but must be the result of sexual selection' (Jehl & Murray 1986). This view is so entrenched that recent comparative studies have used the degree of male-biased sexual dimorphism as a proxy of the strength of sexual selection acting on males (Møller & Birkhead 1994; Barraclough *et al.* 1995).

Although there have been several studies of the present function of sexual dimorphism and trait size, these do not necessarily explain how dimorphism evolved from an ancestral state (Burns 1998). By reconstructing ancestral states across a phylogeny to describe trait size changes, we can help to elucidate the mechanisms involved in the evolution of sexual differences (Burns 1998; Coddington *et al.* 1997). To explore the evolution of sexual dimorphism in birds, we reconstructed ancestral states to describe the direction and extent of changes in wing- and bill-length as well as changes in plumage, breeding environment and parental investment associated with independent evolutionary events in cardueline finches. We used the results of these analyses to test specific hypotheses for the evolution of sexual dimorphism. Cardueline finches are well suited for such an inquiry: there is a large, well-supported phylogeny for the group (Badyaev 1997*a*), several detailed studies of the evolution of sexual dimorphism in the group have been conducted (Andersson 1994; Badyaev 1997*b*; Badyaev & Martin 2000) and the ecology of many species is well known.

2. METHODS

We compared changes in wing-length values between dimorphic species (based on published data; Badyaev 1997*a,b*; Cramp 1992; Ridgway 1901; Palmer 1988; Godfrey 1979) and reconstructed monomorphic node values within the published phylogenies (Badyaev 1997*a*) for each independent case of evolution of sexual dimorphism ($n=15$ species from 126 total species analysed). We defined dimorphism in a trait as a greater than 4% difference between male and female values. Small changes in this value did not qualitatively change our results. We also reconstructed nodal values within the phylogenies for plumage sexual dichromatism (male brightness score–female brightness score), bill-length, breeding elevation, habitat type, mean clutch size and duration of the nestling feeding stage (all values based on published data; Badyaev 1997*a,b*). We restricted the analyses to species in clades (i) that were not polytomous or were polytomous but included four or fewer species, and (ii) where state of the ancestral node or the node immediately preceding the ancestral node was unequivocal. In polytomous clades of four or less, or in clades where the immediate ancestor was equivocal but the preceding node was unequivocal, we randomly selected one extant species for analysis.

One assumption of tracing continuous traits through a phylogeny is that trait reductions are as likely as trait increases. This is supported by numerous selection experiments, which show equivocal evolutionary responses to selection for size increases and decreases among a range of taxa (Falconer & Mackay 1996) and field observations in birds that indicate that both size increases and decreases have occurred over evolutionary time (Price & Boag 1987). As we assume that selection can act on each sex independently, it is important to reconstruct ancestral states for each sex rather than assessing the evolutionary changes in the difference between the sexes in a residual analysis.

We traced ancestral states through the phylogeny using the squared-change parsimony algorithm in MacClade (Maddison & Maddison 1992). We chose to employ the squared-change parsimony algorithm instead of the alternative option, linear parsimony, for two reasons. First, squared-change parsimony has successfully been used to document the evolution of male

Table 1. *Direction and magnitude of wing-length changes associated with evolution of sexual dimorphism*

(M signifies male, F signifies female of the species. Node signifies reconstructed values for the closest unequivocal ancestral node; wing-length values were reconstructed using the square-change parsimony algorithm (see text). Wing-length represents the present extant species morphology. % dim is the percentage sexual dimorphism in extant species. Signs + and − indicate positive and negative changes, respectively, in wing-length between the reconstructed node and the present dimorphic species state. % nodal change indicates the magnitude of the change in morphology between the reconstructed node and the present species morphology.)

species	sex	node (mm)	wing-length (mm)	% dim	sign	% nodal change
Carpodacus cassinii	M	86.18	93	4.26	+	7.61
	F	83.59	89.2		+	6.49
Carduelis spinoides	M	76.27	79.5	4.61	+	4.15
	F	74.58	76		+	1.89
Carduelis yemenensis	M	77.36	79	12.06	+	2.10
	F	74.06	70.5		−	4.93
Carduelis lawrencei	M	67.9	67.5	4.65	−	0.59
	F	65.53	64.5		−	1.58
Serinus syriacus	M	75.6	77.8	4.29	+	2.87
	F	73.01	74.6		+	2.15
Serinus serinus	M	73.17	72.7	4.76	−	0.64
	F	70.64	69.4		−	1.77
Serinus rothschildi	M	76.1	69	9.52	−	9.79
	F	72.92	63		−	14.60
Serinus gularis	M	78.61	82.5	4.43	+	4.83
	F	77.59	79		+	1.80
Linurgus olivaceus	M	73.29	76.5	4.79	+	4.29
	F	71.52	73		+	2.05
Loxia leucoptera	M	96.84	92.1	4.19	−	5.02
	F	94.16	88.4		−	6.31
Leucosticte arctoa atrata	M	107.21	112	6.16	+	4.37
	F	103.39	105.5		+	2.02
Leucosticte branti	M	108.07	117.5	5.86	+	8.36
	F	104.46	111		+	6.07
Pinicola subhimachala	M	102.3	101	7.45	−	1.28
	F	99.15	94		−	5.33
Rhodopechys sanquinea	M	95.67	107.1	4.39	+	11.27
	F	94.16	102.6		+	8.58
Eophona migratoria	M	107.25	102.5	6.77	−	4.53
	F	103.63	96		−	7.64

and female trait changes in a range of taxa, including birds, in a number of recent studies (Coddington *et al.* 1997; Burns 1998). Also, the linear parsimony option depends on a strictly dichotomous tree, the creation of which requires the exclusion of most taxa from analysis because they were in polytomous clades.

3. RESULTS AND DISCUSSION

If sexual dimorphism is driven by male elaboration, we would expect increases in male wing-length (which is highly related to body size) in association with the evolution of dimorphism. Conversely, if dimorphism is produced by female size reduction, we would observe a decrease in female wing-length at each dimorphic event. Our data clearly indicate that sexual dimorphism is just as likely to occur through trait reduction in females ($n = 7$) as increased trait size in males ($n = 9$) (table 1). These 16 cases are randomly distributed across the phylogeny in terms of body size, mating system and taxonomic affinities.

Strikingly, in all but one case (*Carduelis yemenensis*), trait sizes changed in the same direction in both sexes. This indicates that selection acts in the same direction on both sexes (but is more effective in one sex); and/or that selec-

tion on one sex drags along a response in the other by genetic correlation between male and female traits (Lande & Arnold 1985). It is important to stress that our conclusions are based purely on the direction of the size changes and not the absolute magnitude. There are a number of techniques that could be used to reconstruct ancestral values (Cunningham *et al.* 1998), and although these different techniques render slightly different values, they do not alter the direction of the large size changes we have indicated. Hence, we feel our conclusions are robust across a number of methodologies.

It is possible that allometry could skew sexual dimorphism data due to overall trait size changes. However, we found little evidence of allometric effects in the cardueline finches, which is unusual and further highlights the need to test for such effects in studies of dimorphism. Female wing-size and male wing-size were very closely related in a linear regression where the slope of the regression line was approaching unity and the intercept passed very close to the origin ($F_{1,110} = 7626.9$, $p < 0.0001$, $r^2 = 0.986$; female wing-length (mm) = male wing-length (mm) × 0.951 + 2.14 (mm)). We also compared the residuals from this analysis with relative

measures of sexual dimorphism (i.e. difference between male and female divided by average trait size) and found a very close association ($F_{1,110} = 1363.1$, $p < 0.0001$, $r^2 = 0.925$). Hence, the direction of trait size changes *per se* will not have affected sexual dimorphism.

To further evaluate the relationship between sexual selection and the evolution of size dimorphism, we reconstructed changes in plumage sexual dichromatism (male brightness–female brightness) through the phylogeny. Sexual dichromatism in plumage is correlated with degree of sexual selection in birds (Andersson 1994) and if the evolution of size dimorphism we observed was the result of sexual selection on males, we might expect a disproportionately large number of the species in table 1 to have also increased in plumage sexual dichromatism. Of ten dimorphic species in table 1 available for analysis, however, only two (20%) increased in plumage sexual dichromatism, while 15 out of 43 (34.8%) other species in the phylogeny increased in plumage sexual dichromatism. If we assume a null model of random allocation of evolutionary transitions among our taxa, the association of evolutionary transitions in size dimorphism and colour dichromatism is no more than that expected by chance (Fisher two-tailed exact test, $p = 0.47$). Considering only those species in table 1 in which size dimorphism evolved due to a relatively larger increase in males than females, two out of five species (40%) increased in sexual dichromatism. This value is close to the corresponding value of 34.8% observed in the monomorphic species in the phylogeny, although the sample sizes are small.

We also reconstructed sexual plumage dichromatism in the phylogeny using different transition state probabilities to make the loss of sexual dichromatism more likely than gain of dichromatism, which may be a more realistic assumption for such an analysis (Cunningham *et al.* 1998). However, there was no qualitative change in the pattern when we made losses of sexual dichromatism twice (Fisher two-tailed exact test, $p = 1.0$) and four times (Fisher two-tailed exact test, $p = 1.0$) as likely as gains. The lack of association between transitions in size dimorphism and plumage dichromatism indicates separate evolutionary processes and causes for sexual dimorphism and dichromatism in these taxa, further supporting our suggestion that sexual selection alone cannot fully explain sexual size dimorphism.

To examine whether the pattern we noted for finches applies to a broader selection of birds, we applied the same techniques to wing-length data and phylogenetic information for another 16 genera and 87 species of birds from a range of taxonomic groups (*Acrocephalus* warblers, *Sylvia* warblers, *Piranga*, Anatidae and Anserinae). We identified 12 independent occurrences of the evolution of normal sexual dimorphism; six resulted from males increasing in size at a greater rate than females, whereas the remaining six arose from females decreasing in size at a faster rate than males. Hence, as in the detailed case of the finches, male-biased sexual size dimorphism is as likely to occur due to females decreasing in size as males getting larger. In all these species the sexes changed size in the same direction, which is consistent with a genetically correlated response to selection in the non-target sex (Lande & Arnold 1985). This broader analysis also suggests that the

patterns we have revealed may be generally applicable to sexual size differences in birds.

Our finding that directional sexual selection on increased male body size cannot alone explain the evolution of male-biased (normal) sexual size dimorphism in birds suggests that alternative hypotheses may apply more broadly than previously thought. Therefore, we tested two other prominent hypotheses for the evolution of sexual dimorphism: ecological niche partitioning between the sexes and reproductive benefits associated with reduced size in females (Andersson 1994). The ecological niche-partitioning hypothesis (Selander 1966) posits that sexual dimorphism may arise in response to selection on males and females to exploit different environmental niches, thereby reducing competition for resources. For finches, bills are an integral foraging mechanism, which can respond rapidly and dramatically over evolutionary time to shifts in food resources (Price *et al.* 1984; Björklund 1991). If body-size dimorphism arose in response to exploitation of different food resources by males and females, we would expect those species that evolved body-size dimorphism to have also evolved bill-size dimorphism. In contradiction to this prediction, however, only 1 out of the 13 species that evolved body-size dimorphism also evolved bill-size dimorphism (7.7%), which is lower but not significantly different from the rate of 9.8% (5/51) in the other species in the phylogeny. (Fisher two-tailed exact test, $p = 1.0$). The observed constancy in bill-length despite sometimes dramatic shifts in body size among the species in table 1 suggests that ecological niche partitioning cannot explain the evolution of body-size dimorphism in most of the species. Also, the ecological niche-partitioning hypothesis predicts that males and females are equally likely to become the larger sex, yet males are larger than females in all cases of sexual dimorphism we observed.

To further test if ecological change was associated with evolution of size dimorphism, we reconstructed maximum and minimum breeding elevation and habitat type for the species in the phylogeny. Twelve out of the 15 species in table 1 were available for these analyses. Species that evolved dimorphism were no more likely to have changed in maximum breeding elevation (Fisher two-tailed exact test, $p = 1.0$) or minimum breeding elevation (Fisher two-tailed exact test, $p = 1.0$) than species that did not evolve dimorphism. Similarly, frequency of habitat change did not differ between the species in table 1 and the remaining species in the phylogeny (Fisher two-tailed exact test, $p = 0.99$). These results, in conjunction with the stability of bill size discussed above, render it unlikely that sexual dimorphism arose in response to a shift in food sources due to an elevation or habitat change.

It is also possible that directional selection on reduced female body size for increased breeding efficiency resulted in the evolution of size dimorphism, especially for those species in which dimorphism arose as a result of females reducing in size more than males (Downhower 1976; Price 1984). We reconstructed clutch size and number of days spent feeding nestlings to determine if those species that evolved dimorphism increased their breeding efficiency via increased clutch size or reduced nestling stage, as might be predicted by the reduced female body-size hypothesis. Clutch size did not change

for any of the species that evolved size dimorphism and were available for this analysis ($n = 7$). Similarly, changes in the duration of nestling stage did not differ significantly between species that evolved dimorphism and those that did not (Fisher two-tailed exact test, $p = 0.26$), even when looking only at those dimorphic species in which females decreased in size more rapidly than did males. Finally, it is possible that directional sexual selection on reduced female size led to the pattern of size dimorphism we observed, but we could not test this possibility with the available data.

It is commonly assumed in both the sexual selection and sexual dimorphism literature that increased male size (relative to females) has resulted from directional (sexual) selection acting more intensely on males than on females. Our study shows that this is not a safe assumption to make without phylogenetic evidence to support the case. It may still be the situation that sexual selection tends to increase male size, but in *ca.* 50% of the cases we studied there is more intense net selection on females to decrease in size, which could result from natural and/or sexual selection acting on females. Our data suggest that selection for reduced size in females can often drive the evolution of male-biased sexual dimorphism and that directional selection on females should be considered in concert with selection on males in any study of sexual dimorphism. We conclude that no single hypothesis provides a universal explanation for the evolution of sexual dimorphism in birds, but that a balance of various selective forces should be tested using a phylogenetic approach.

REFERENCES

Andersson, M. 1994 *Sexual selection.* Princeton University Press.

Badyaev, A. V. 1997*a* Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. *Behav. Ecol.* **8**, 675–699.

Badyaev, A. V. 1997*b* Avian life history variation along altitudinal gradients: an example with carduline fiches. *Oecologia* **111**, 365–374.

Badyaev, A. V. & Martin, T. E. 2000 Sexual dimorphism in relation to current selection in the house finch. *Evolution* **54**, 987–997.

Barraclough, B. G., Harvey, P. H. & Nee, S. 1995 Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. Lond.* B **259**, 211–215.

Björklund, M. 1991 Patterns of morphological variation among carduline finches (Fringillidae: Carduelinae). *Biol. J. Linn. Soc.* **43**, 239–248.

Burns, K. J. 1998 A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus male plumage. *Evolution* **52**, 1219–1224.

Coddington, J. A., Hormiga, G. & Scharff, N. 1997 Giant female or dwarf male spiders? *Nature* **385**, 687–688.

Cramp, S. (ed.) 1992 *The birds of the Western Palearctic.* Oxford University Press.

Cunningham, C. W., Omland, K. E. & Oakley, T. H. 1998 Reconstructing ancestral character states: a critical appraisal. *Trends Ecol. Evol.* **13**, 361–366.

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

Downhower, J. F. 1976 Darwin's finches and the evolution of sexual dimorphism in body size. *Nature* **263**, 551–563.

Falconer, D. S. & Mackay, T. F. C. 1996 *Introduction to quantitative genetics.* Harlow: Longman.

Godfrey, W. E. 1979 *The birds of Canada.* Ottawa: National Museums of Canada.

Jehl, J. R. & Murray, B. G. 1986 The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. In *Current ornith*ology, vol. 3 (ed. R. F. Johnstone), pp. 1–86. New York: Plenum.

Lande, R. & Arnold, S. J. 1985 Evolution of mating preference and sexual dimorphism. *J. Theor. Biol.* **117**, 651–664.

Maddison, W. P. & Maddison, D. R. 1992 *MacClade 3.0.* Sunderland, MA: Sinauer Associates.

Møller, A. P. & Birkhead, T. R. 1994 The evolution of plumage brightness in birds is related to extra-pair paternity. *Evolution* **48**, 1089–1100.

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

Palmer, R. S. (ed.) *Handbook of North American birds*, vol. 2. New Haven, CT: Yale University Press.

Price, T. D. 1984 The evolution of sexual size dimorphism in Darwin's finches. *Am. Nat.* **123**, 500–518.

Price, T. D., Grant, P. R., Gibbs, H. L. & Boag, P. T. 1984 Recurrent patterns of natural selection in a population of Darwin's finches *Nature* **309**, 787–789.

Price, T. D. & Boag, P. T. 1987 Selection in natural populations of birds. In *Avian genetics* (ed. P. A. Buckley & F. Cooke), pp. 257–287. London: Academic Press.

Ridgway, R. 1901–1919. *The birds of the North and Middle America: a descriptive catalog of the higher groups, genera, species and subspecies of birds known to occur in North America, from the Arctic lands to the isthmus of Panama, the West Indies and other islands of the Caribbean Sea, and the Galapagos Archipelago. Part I. Family Fringillidae—The finches.* Washington, D.C: United States Government Printing Office.

Selander, R. K. 1966 Sexual dimorphism and differential niche utilization in birds. *Condor* **68**, 113–151.