Degree of mutual ornamentation in birds is related to divorce rate

Ken Kraaijeveld†

Department of Zoology, University of Melbourne, VIC 3010, Australia (*k.kraaijeveld@ucl.ac.uk*)

Many bird species have ornaments that are expressed equally in both sexes. I use comparative analysis to investigate why some monomorphic birds are highly ornamented, whereas others are drab. The results show a significant positive association between the degree of mutual ornamentation and divorce rate. This result is robust to the removal of the effects of phylogeny, site fidelity, residency, coloniality, nest type, mortality, body size and body-size dimorphism. The level of extra-pair paternity was not related to the degree of mutual ornamentation. I argue that these results are compatible with a process of mutual sexual selection, in which both sexes compete for access to mates. The coupled evolution of ornamentation and divorce rate, from the probable ancestral state of a high degree of ornamentation and a low divorce rate, appears to result mainly from a loss of ornamentation under mate fidelity.

Keywords: mutual sexual selection; mutual ornamentation; divorce rate; comparative analysis

1. INTRODUCTION

Extravagant ornamentation in animals is generally assumed to be the result of sexual selection (Darwin 1871; Andersson 1994). Most studies focus on species where one of the sexes is highly ornamented, whereas the other sex is inconspicuous. However, in many species, both the male and the female are highly ornamented. There is much variation in the degree of ornamentation among sexually monomorphic species. Although the factors affecting the degree of sexual dimorphism have been investigated in a number of comparative studies (Møller & Birkhead 1994; Owens & Hartley 1998; Cuervo & Møller 1999; Dunn *et al.* 2001), the question of why some sexually monomorphic species are highly ornamented, but others are not, has received little attention.

Female ornamentation may be a genetic consequence of sexual selection on males (Lande & Arnold 1985). Interspecific variation in the degree of mutual ornamentation may thus be caused by variation in the strength of sexual selection on males. However, a number of phylogenetic studies in birds have shown that evolutionary changes between dimorphism and monomorphism have occurred frequently and in both directions (reviewed in Wiens 2001), indicating that such changes are relatively unconstrained by genetic correlations (Amundsen 2000).

If both sexes compete for access to mates, sexual selection may operate equally on both sexes (Huxley 1914; Jones & Hunter 1993). Recent studies on crested auklets, *Aethia cristatella*, have shown that individuals with larger crest ornaments are more attractive to the opposite sex and are dominant in social competition for mates (Jones & Hunter 1993, 1999). At present, mutual sexual selection has not been demonstrated in other species with equally ornamented sexes. If the strength of mutual sexual selection is a more general explanation for the interspecific variation in the degree of mutual ornamentation in birds, it

should be possible to find a correlation between ornamentation and some measure of sexual-selection intensity at an interspecific level.

Comparative studies in birds have shown that the degree of sexual dimorphism is related to the type of parental care, the social mating system and the level of extra-pair paternity (EPP) (Møller & Birkhead 1994; Owens & Hartley 1998; Cuervo & Møller 1999; Dunn *et al.* 2001). Most sexually monomorphic bird species have biparental care, are socially monogamous and have low levels of extra-pair paternity, although exceptions do occur (Trail 1990). Under social and sexual monogamy, the strength of mutual sexual selection may vary with the frequency of mate choice, assuming that the variation in the number of breeding attempts per lifetime is similar in males and females. High divorce rates should lead to more frequent competition for mates and might thus be related to greater mutual ornamentation.

If mutual ornaments signal social dominance in competition for mates, they may also signal dominance in non-sexual contexts. Social competition for resources such as food and nest sites could lead to ornamentation in the same way as competition for mates (Tanaka 1996). Such signals are thought to be particularly beneficial when there is regular competition with unfamiliar individuals (Whitfield 1987). This situation is likely in colonial species and species with low site fidelity. In addition, social competition for nest sites may be most intense in cavity-nesting species, or in migratory species that have to re-establish territories each year.

The aims of this study were to investigate whether mutual ornamentation in birds is related to social competition for mates (divorce) and other resources (coloniality, site fidelity, nest sites and residency), while controlling for the effects of phylogeny and other confounding variables; and, if so, to infer the scenario for the coupled evolution of mutual ornamentation and mate fidelity.

† Present address: The Galton Laboratory, Department of Biology, University College London, Wolfson House, 4 Stephenson Way, London NW1 2HE, UK.

2. MATERIAL AND METHODS

(a) Data collection

Data were collated for 119 species of bird for which estimates of divorce rate were available (see electronic Appendix A; available on The Royal Society's Publications Web site). The criterion for inclusion in the analysis was that the variation in coloration and ornamentation between the sexes did not exceed the variation within the sexes. I controlled for sexual size dimorphism by including it as an independent variable in the multivariate analysis. The blue tit, *Parus caeruleus*, was excluded from the analysis because it is known to be dimorphic in the, for humans invisible, ultraviolet (UV) light range (Hunt *et al.* 1998). Data on UV reflection were not available for other species in this study. Ornamentation was scored using colour plates in handbooks and field guides (National Geographic Society 1987; Slater *et al.* 1989; Del Hoyo *et al.* 1992–1997; Sinclair *et al.* 1996; Mullaney *et al.* 1999). I scored overall ornamentation on a scale from 0 to 7, by scoring three types of ornaments (feather, bare parts and plumage) separately and then summing the scores. Different ornament types may have different signalling functions (Møller & Pomiankowski 1993), and I therefore also considered each type of ornament separately. Feather ornaments were defined following Cuervo & Møller (1999) as feathers larger than expected for a particular feather tract, as compared with other feathers in the same species or equivalent feathers in closely related species. Feathers shaped in a way that was conspicuous and different from that expected for a particular tract were also scored as ornamental. Ornamental feathers were scored as: 0 (absent); 1 (longest ornamental feather less than twice the length of a normal feather in the same tract); or 2 (longest ornamental feather more than twice the length of a normal feather in the same tract). Bare parts included the bill, eyes, orbital rings, legs and bare skin patches, and were scored as: 0 (no brightly coloured bare parts); 1 (at least one of the bare parts coloured, but not highly conspicuous); or 2 (at least one of the bare parts bright and conspicuous). Species with appendages on the head were scored as 2, regardless of further coloration. Head appendages were expected to have a strong signal function, since in many species opponents face each other during contests (e.g. red frontal shield in the moorhen, *Gallinula chloropus*; Petrie 1988). Plumage patches were scored by visual inspection using the following categories: 0 (no ornamental coloration); 1 (0–10% of plumage colour ornamental); 2 (10–50% of plumage colour ornamental); or 3 (more than 50% of plumage colour ornamental). Any ornamental feathers were scored again if they were coloured, so, for example, a bright yellow crest would be scored as 3, whereas a similar-sized black crest would be scored as 2.

Two observers that were unaware of the purpose of the study carried out the scoring. This method of scoring ornamentation was highly repeatable (intraclass correlation coefficient (Zar 1999, p. 404): $r_i = 0.90$, $F = 18.36$, $p < 0.0001$). In instances where the two observers disagreed, their scores were averaged. The scores for the three types of ornament were then summed to give the final ornamentation score. To verify whether the main results were robust to an alternative scoring system, three different observers arbitrarily scored all species as either 'ornamented' or 'not ornamented' (hereafter termed 'binary ornament score'). The criterion was simply whether the observer considered a species to have a conspicuous (structural or colourful) ornament, or not. When the three observers disagreed, I used the score chosen by two out of the three. These

ornament scores were repeatable for each observer (pairwise $r_i = 0.48$, 0.40 and 0.48, all $p < 0.001$).

The main aim of this study was to investigate correlated evolution between mutual ornamentation and divorce rate, coloniality, site fidelity, nest type and residency. I used multivariate statistics to control for four behavioural and ecological variables that may influence such an association (female weight, body size dimorphism, mortality and EPP). Mortality was included in the analysis because it may be related to divorce rate. Cézilly & Nager (1995) found a weak negative correlation between divorce rate and survival rate, but Ens *et al.* (1996) using a larger dataset found no clear relationship between divorce rate and mortality. EPP is positively correlated with divorce (Cézilly & Nager 1995). All species in the analysis had biparental care and were socially monogamous. Divorce rate was calculated as the number of pairs where one or both partners bred with a different partner the following year, when the previous partner was known to be alive, divided by the total number of pairs for which both partners were known to be alive (Black 1996; Cézilly *et al.* 2000). When estimates from more than one study were available, the mean value, weighted according to the number of pair-years in each study, was used. Within-season mate switching was not included, as such data are scarce (Cézilly & Nager 1995). There was no significant correlation between divorce rate (arcsine transformed) and the number of pair-years (Pearson's $r = -0.16$, $p = 0.10$), indicating that the data were not significantly biased. Coloniality was scored as in Dubois *et al.* (1998): 1 = typically breeds in large colonies; 0 = solitary or forming loose aggregations. Measures for residency, site fidelity and mortality follow Black (1996, p. 396)—residency: 0 = resident year-round on territory (seabirds are classified as resident when they visit specific nest sites throughout the year); 1 = semi-resident or migratory; and site fidelity: 0 = no strong fidelity (this includes seabirds that return to the same colony, but nest anywhere in that colony); 1 = strong site fidelity (the majority of individuals return to the nesting site of the previous year). Mode of nesting was scored as in Cuervo & Møller (1999): 1 = nesting in cavity or dome nest; 0 = open nest. Female weight was taken as a measure of body size, and the residuals from the regression of male weight on female weight were used as a measure of body-size dimorphism. I defined EPP as the proportion of offspring not fathered by the social father, as determined by DNA fingerprint analysis (Owens & Hartley 1998).

To approach normality, the ornament scores and female weights were log-transformed and divorce rate, mortality rate and EPP data were arcsine-transformed before analysis. Statistical tests were performed in SYSTAT 7 (Systat 1997).

(b) Comparative methods

The use of raw species data in comparative analysis is problematic, because closely related species may share characteristics owing to shared ancestry (Harvey & Pagel 1991; Nunn & Barton 2001). To produce data that were phylogenetically independent under a specific evolutionary model, I calculated standardized linear contrasts (Felsenstein 1985; Harvey & Pagel 1991) as implemented by the computer package CAIC (Purvis & Rambaut 1995). I assumed a phylogenetic topology based on Sibley & Ahlquist (1990). Additional resolution below the family level was obtained from other sources (Sheldon *et al.* 1995; Nunn *et al.* 1996; Livezey 1997; Bretagnolle *et al.* 1998). Because the values provided by Sibley & Ahlquist (1990) do not categorically establish the evolutionary time elapsed between nodes, and because the phylogeny I used was a composite of

several phylogenies, branch lengths were made equal. This assumes a punctuated model of evolution and is an accepted default procedure when branch lengths are not available (Purvis *et al.* 1994). Several studies have found that the assumption of equal branch lengths did not affect the results qualitatively (Møller *et al.* 1998; Nunn 1999; Poulin 1999). To examine whether the main association was independent of the phylogenetic hypothesis used, I constructed a different phylogeny based on recent mtDNA data (Mindell 1997; Siegel-Causey 1997; Braun & Brumfield 1998; Heidrich *et al.* 1998; Joseph *et al.* 1999; Saunders & Edwards 2000; Sheldon *et al.* 2000; Ruokonen *et al.* 2000). The main differences from the phylogeny based on Sibley & Ahlquist (1990) were: basal placement of the Passeriformes and re-organization of the Pelecaniformes, Anseriformes and Procellariidae. In instances where the information was incomplete, I used the phylogeny based on Sibley & Ahlquist (1990). Branch lengths were again made equal. Because the mtDNA-based phylogeny could not be completely resolved, and because the basal placement of the passerines is unconventional, the main analysis is based on the phylogeny of Sibley & Ahlquist (1990). I used MACCLADE 3.08 (Maddison & Maddison 1992) to estimate the most probable ancestral state of mutual ornamentation and divorce rate by maximum parsimony (Swofford & Maddison 1987).

I fitted multivariate general linear models to control for potentially confounding factors. However, estimates of EPP were available for only 22 out of the 119 species. Sample sizes for the other variables ranged from 84 to 119. Adding all variables, except EPP, into one model reduced the sample size to 56 species. Note that this change in sample size also changed the species that were examined, and, thus, different results in different models may be caused by sample size or species differences (Dunn *et al.* 2001). To address this problem, I examined models with both the largest (bivariate) and the smallest (multivariate—excluding EPP) sample sizes. The multivariate analysis was subsequently tested with a backward stepwise model (p to enter and remove = 0.10). All models were forced through the origin (Garland *et al.* 1992). For the bivariate analyses, the CRUNCH algorithm in CAIC was used when the independent variables were continuous and the BRUNCH algorithm was used when they were dichotomous. The CRUNCH procedure calculates contrasts at each of the nodes in the phylogeny. The BRUNCH procedure identifies nodes at which the dichotomous variable changes from 0 to 1 and calculates the contrast in the continuous variable at each of those nodes. A positive contrast means that the continuous variable changes in the same direction as the dichotomous variable. I tested these contrasts against a null hypothesis of no net change using a one-sample t -test. As the BRUNCH function allows only one dichotomous variable to be included at a time, I used CRUNCH for the multivariate analysis, which treats dichotomous variables as if they were continuous. The results of bivariate analyses using CRUNCH instead of BRUNCH were qualitatively similar. Furthermore, the residuals of these bivariate regressions followed a normal distribution and did therefore not violate the assumptions of regression as advocated by Grafen (1989). In the analysis of the binary ornament scores, I used BRUNCH to determine the nodes at which a switch from 'non-ornamented' to 'ornamented' occurred and calculated the change in divorce rate at those nodes. I tested these contrasts against a null hypothesis of no net change using a one-sample t -test.

To test the temporal orderings and the directions of evolutionary change of mutual ornamentation and divorce rate, I used the discrete-variable method of Pagel (1994, 1999a,b). This

method uses a continuous-time Markov model to describe evolutionary changes along each branch of a phylogenetic tree (Pagel 1994). As variables need to be dichotomous for this method, I used the mean of the data as a threshold (Cézilly *et al.* 2000; mean ornamentation = 1.74, mean divorce rate = 0.24). As the method can investigate only one variable pair at a time, controlling for additional variables was not possible. I tested models of evolution in which certain types of character transition were excluded *a priori*, by forcing the relevant transition parameter to zero. The fit of the reduced model in which one of the parameters is constrained was then compared with that of the full model using a likelihood-ratio test (Pagel 1994; Cézilly *et al.* 2000). See Pagel (1994, 1997, 1999a,b) for more information on this method.

3. RESULTS

(a) Independent contrasts

At the species level, there was a highly significant positive association between mutual ornamentation and divorce rate (linear regression: $n = 119$, $r^2 = 0.14$, $F = 19.25$, $p < 0.0001$). The analysis of independent contrasts confirmed this relationship (table 1; figure 1). However, the association was weaker than in the species-level analysis, indicating that the species-level result suffers from phylogenetic non-independence. The removal of two outlying data points (leverage = 0.12 and 0.11) substantially strengthened the association ($n = 116$, $r^2 = 0.06$, $F = 7.59$, $p = 0.007$). These two outlying data points concerned recent nodes within the Passeriformes (Sylviidae and Hirundinidae). None of the other independent variables had a significant effect on ornamentation in the analysis of independent contrasts (table 1). In a multivariate general linear model, divorce rate was the most significant predictor of ornamentation (table 1). Only divorce rate and nest type were entered into the final stepwise model (individual p -values of 0.0001 and 0.02, respectively). Sixteen independent contrasts were identified using the binary ornament scores. There was a positive contrast in the divorce rate at 12 of these ($t_{15} = 2.56$, $p = 0.02$), indicating that the association between mutual ornamentation and divorce rate is not an artefact of the way in which the ornaments were scored. The association between mutual ornamentation and divorce rate was also significant when using the mtDNA-based phylogeny ($n = 118$, $r^2 = 0.04$, $F = 4.91$, $p = 0.03$).

All three types of ornament showed a significant positive correlation with divorce rate in multivariate models ($0.02 < p < 0.05$). In separate regressions, only bare-part coloration was significantly correlated with divorce rate ($n = 118$, $F = 3.99$, $p = 0.04$). Feather ornamentation was significantly correlated with residency ($t = 2.97$, $p = 0.005$) in the multivariate analysis, but not in the separate regression.

(b) Evolutionary pathways

Judging by parsimony, a high ornamentation rate appears to be the ancestral state (although this is ambiguous when using the mtDNA-based phylogeny). Both phylogenies further suggest that divorce rates were low in ancestral birds. The discrete-variables method was used to assess the probable temporal ordering of changes in ornamentation and divorce rate (figure 2). From the most

Table 1. General linear models of mutual ornamentation in relation to nine independent variables, using independent contrasts generated in CAIC.

(Variables entered into the final stepwise model are indicated in bold (individual p -values not shown). n refers to contrasts, not species. Categorical variables are indicated with an asterisk.)

(a) separate models

variable	n	r^2	β	d.f.	F/t	p
divorce rate	118	0.03	0.91	1	$F = 4.09$	0.04
site fidelity*	13				$t = -0.22$	0.83
residency*	20				$t = -0.83$	0.42
coloniality*	18				$t = 1.01$	0.32
nest type*	13				$t = -0.36$	0.73
mortality	83	0.00	-0.22	1	$F = 0.04$	0.84
female mass	101	0.02	0.00	1	$F = 1.91$	0.17
body-mass dimorphism	99	0.01	0.00	1	$F = 0.97$	0.33
extra-pair paternity	21	0.01	1.27	1	$F = 0.23$	0.64

(b) multivariate model ($n = 55$, $r^2 = 0.43$, $F_{8,47} = 3.48$, $p = 0.003$)

variable	β	t	p
divorce rate	3.31	4.10	0.0002
site fidelity*	-0.71	-1.37	0.17
residency*	0.16	0.35	0.73
coloniality*	-0.56	-1.68	0.09
nest type*	1.06	2.28	0.03
mortality	-0.96	-0.77	0.44
female mass	0.00	0.53	0.60
body-mass dimorphism	0.00	-0.72	0.48

Figure 1. Mutual ornamentation in relation to divorce rate among bird species in which the sexes are similar in appearance, using independent contrasts as data points.

probable ancestral state of a high level of mutual ornamentation and a low divorce rate, mutual ornamentation was lost, while divorce rate remained low (state 2; $\chi^2_1 = 14.04$, $p < 0.001$). From state 2, there was a transition towards a high divorce rate with a low degree of mutual ornamentation (state 3; $\chi^2_1 = 10.45$, $p < 0.005$). The ancestral state can also re-evolve from a high degree of mutual ornamentation and a high divorce rate (state 4; $\chi^2_1 = 5.662$, $p < 0.025$; figure 2).

4. DISCUSSION

The results of this study show that extravagant mutual ornamentation occurs most frequently in species with high divorce rates. Species in which both sexes are drab tend to have low divorce rates. The result was slightly weaker after controlling for phylogeny, which was largely caused by the strong influence of two outlying data points. Both these outlying data points concerned recent nodes within the Passeriformes, suggesting that the relationship is strongest in the non-passerines. Divorce is likely to lead to competition for mates in both sexes and is thus a measure of mutual sexual selection. EPP, however, is expected to result in stronger sexual selection on males than on females (Møller & Birkhead 1994). EPP had no effect on mutual ornamentation, which is not compatible with the idea that mutual ornamentation is maintained by sexual selection on males (and a genetic correlation in females), but supports the mutual sexual selection hypothesis.

Although the relation between the degree of mutual ornamentation and the divorce rate was significant in all analyses, it left much of the variation in the degree of ornamentation unexplained (divorce rate explained 14% of the variation in ornamentation in the raw species data and 3% in the independent contrasts). The results of the discrete-variable analysis indicated that mutual ornamentation and divorce rate have changed in a dependent (discussed below) as well as an independent fashion. Other factors may therefore play a part in the evolution and maintenance of mutual ornamentation. One such factor may be

Figure 2. Flow diagram tracing the most likely scenario for the coupled evolution of mutual ornamentation and divorce rate among bird species in which the sexes are similar in appearance. State 1 corresponds to the most probable ancestral state. Bold arrows, highly significant pathways ($p < 0.005$); solid arrows, significant pathways ($p < 0.05$); dashed arrows, non-significant pathways.

social competition for resources, such as nest sites. This is supported by the positive relation between nest type and mutual ornamentation in the multivariate model, as cavity nest sites might be in shorter supply and thus the subject of more competition than open nest sites. None of the other factors considered in this study had a consistent effect on mutual ornamentation. Resources that are the subject of intense social competition are likely to be highly species-specific, not easily generalized and therefore difficult to study in a comparative analysis.

When analysed individually, all three types of mutual ornament showed a positive relationship with divorce rate. When other factors were controlled for, residency was positively correlated with feather ornamentation. Migratory species need to re-establish breeding territories each year and may perhaps do so using feather ornaments. Why feather ornaments would be more useful than other ornaments in such a situation remains to be established.

The correlated evolution of mutual ornamentation and divorce rate from an ancestral state must be examined in the context of evolutionary time (Björklund 1991). My results suggest that ancestral birds were mutually ornamented. This is supported by the finding of fossils of ancient flamingo-like birds in deposits from the Cretaceous (Swinton 1965; Van Tyne & Berger 1976), the modern descendants of which are all highly ornamented. Furthermore, low divorce rates are ancestral. The ancestral state may also re-evolve from a state of a high degree of ornamentation and a high divorce rate (state 4 in figure 2). This transition is probably most important in the Ciconiiformes, for which the ancestral state is a high divorce rate (Dubois *et al.* 1998; Cézilly *et al.* 2000; confirmed in this study). In this group, the transition towards low divorce rates was probably preceded by the evolution of lower degrees of coloniality (Dubois *et al.* 1998) and

higher degrees of site fidelity (Cézilly *et al.* 2000). The most significant shift away from the probable ancestral state was towards lower degrees of mutual ornamentation, while the divorce rate remained low (state 2). Mate fidelity meant that many individuals would already be paired at the start of the breeding season and would not have to compete for access to a new mate. This reduces the need for elaborate ornaments that influence the outcome of sexual competition. Because such ornaments are likely to be costly (Zahavi 1975), they are not favoured by natural selection. Once natural selection against ornamentation was no longer counterbalanced by mutual sexual selection, mutual ornamentation was lost in many species.

The author thanks M. Symonds, F. Cézilly, F. Kraaijeveld-Smit, A. Poiani, D. Dowling, R. Mulder and two anonymous referees for providing helpful comments on earlier drafts of this paper. B. Stout, G. Nuechterlein, W. Piper and O. Overdijk kindly provided published or unpublished data for inclusion in the analysis. F. Kraaijeveld-Smit, W. van Dongen, E. van Willigenburg and E. van Lieshout assisted in the scoring of the ornaments. M. Pagel kindly provided a copy of the DISCRETE program. This research was supported by grants from the Stuart Leslie Bird Research Fund and the Holsworth Wildlife Research Fund.

REFERENCES

- Amundsen, T. 2000 Why are female birds ornamented? *Trends Ecol. Evol.* **15**, 149–155.
- Andersson, M. 1994 *Sexual selection*. Princeton University Press.
- Björklund, M. 1991 Evolution, phylogeny, sexual dimorphism and mating system in the grackles (*Quiscalus* spp.: Icterinae). *Evolution* **45**, 608–621.
- Black, J. M. (ed.) 1996 *Partnerships in birds*. Oxford University Press.

- Braun, M. J. & Brumfield, R. T. 1998 Enigmatic phylogeny of skuas: an alternative hypothesis. *Proc. R. Soc. Lond. B* **265**, 995–999. (DOI 10.1098/rspb.1998.0389.)
- Bretagnolle, V., Attié, C. & Pasquet, E. 1998 Cytochrome-B evidence for validity and phylogenetic relationships of *Pseudobulweria* and *Bulweria* (Procellariidae). *Auk* **115**, 188–195.
- Cézilly, F. & Nager, R. G. 1995 Comparative evidence for a positive association between divorce and extra-pair paternity in birds. *Proc. R. Soc. Lond. B* **262**, 7–12.
- Cézilly, F., Dubois, F. & Pagel, M. 2000 Is mate fidelity related to site fidelity? A comparative analysis in Ciconiiforms. *Anim. Behav.* **59**, 1143–1152.
- Cuervo, J. J. & Möller, A. P. 1999 Ecology and evolution of extravagant feather ornaments. *J. Evol. Biol.* **12**, 986–998.
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London: John Murray.
- Del Hoyo, J., Elliot, A. & Sargatal, J. (eds) 1992–1997 *Handbook of the birds of the world*, vol. 1–4. Barcelona: Lynx edicions.
- Dubois, F., Cézilly, F. & Pagel, M. 1998 Mate fidelity and coloniality in waterbirds: a comparative analysis. *Oecologia* **116**, 433–440.
- Dunn, P. O., Whittingham, L. A. & Pitcher, T. E. 2001 Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* **55**, 161–175.
- Ens, B. J., Choudhury, S. & Black, J. M. 1996 Mate fidelity and divorce in monogamous birds. In *Partnerships in birds: the study of monogamy* (ed. J. M. Black), pp. 344–395. Oxford University Press.
- Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Garland Jr, T., Harvey, P. H. & Ives, A. R. 1992 Procedures for the analyses of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32.
- Grafen, A. 1989 The phylogenetic regression. *Proc. R. Soc. Lond. B* **236**, 119–157.
- Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford University Press.
- Heidrich, P., Amengual, J. & Wink, M. 1998 Phylogenetic relationships in Mediterranean and North Atlantic shearwaters (Aves: Procellariidae) based on nucleotide sequences of mtDNA. *Biochem. Syst. Ecol.* **26**, 145–170.
- Hunt, S., Bennett, A. T. D., Cuthill, I. C. & Griffiths, R. 1998 Blue tits are ultraviolet tits. *Proc. R. Soc. Lond. B* **265**, 451–455. (DOI 10.1098/rspb.1998.0316.)
- Huxley, J. S. 1914 The courtship habits of the great crested grebe *Podiceps cristatus*; with an addition to the theory of sexual selection. *Proc. Zool. Soc. Lond.* **35**, 491–562.
- Jones, I. L. & Hunter, F. M. 1993 Mutual sexual selection in a monogamous seabird. *Nature* **362**, 238–239.
- Jones, I. L. & Hunter, F. M. 1999 Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament. *Anim. Behav.* **57**, 521–528.
- Joseph, L., Lessa, E. P. & Christidis, L. 1999 Phylogeny and biogeography in the evolution of migration: shorebirds of the *Charadrius* complex. *J. Biogeogr.* **26**, 329–342.
- Lande, R. & Arnold, S. J. 1985 Evolution of mating preferences and sexual dimorphism. *J. Theor. Biol.* **117**, 651–664.
- Livezey, B. C. 1997 A phylogenetic classification of waterfowl (Aves: Anseriformes), including selected fossil species. *Ann. Carnegie Mus.* **66**, 457–496.
- Maddison, W. P. & Maddison, D. R. 1992 *MACCLADE*. Sunderland, MA: Sinauer.
- Mindell, D. P. 1997 Phylogenetic relationships among and within select avian orders based on mitochondrial DNA. In *Avian molecular evolution and systematics* (ed. D. P. Mindell), pp. 213–247. San Diego, CA: Academic Press.
- Møller, A. P. & Birkhead, T. R. 1994 The evolution of plumage brightness in birds is related to extra-pair paternity. *Evolution* **48**, 1089–1100.
- Møller, A. P. & Pomiankowski, A. 1993 Why have birds got multiple sexual ornaments. *Behav. Ecol. Sociobiol.* **32**, 167–176.
- Møller, A. P., Sorci, G. & Erritzze, J. 1998 Sexual dimorphism in immune defence. *Am. Nat.* **152**, 605–619.
- Mullarney, K., Svensson, L., Zetterström, D. & Grant, P. J. 1999 *Bird guide*. London: Collins.
- National Geographic Society 1987 *Field guide to the birds of North America*. Washington: National Geographic Society.
- Nunn, C. L. 1999 The number of males in primate social groups: a comparative test of the socioecological model. *Behav. Ecol. Sociobiol.* **46**, 1–13.
- Nunn, C. L. & Barton, R. A. 2001 Comparative methods for studying primate adaptation and allometry. *Evol. Anthropol.* **10**, 81–98.
- Nunn, G. B., Cooper, J., Jouventin, P., Robertson, C. J. R. & Robertson, G. G. 1996 Evolutionary relationships among extant albatrosses (Procellariiformes: Diomedidae) established from complete cytochrome-B gene sequences. *Auk* **113**, 784–801.
- Owens, I. P. F. & Hartley, I. R. 1998 Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. Lond. B* **265**, 397–407. (DOI 10.1098/rspb.1998.0308.)
- Pagel, M. 1994 Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond. B* **255**, 37–45.
- Pagel, M. 1997 Inferring evolutionary processes from phylogenies. *Zool. Scripta* **26**, 331–348.
- Pagel, M. 1999a Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884.
- Pagel, M. 1999b The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Syst. Biol.* **48**, 612–622.
- Petrie, M. 1988 Intraspecific variation in structures that display competitive ability: large animals invest relatively more. *Anim. Behav.* **36**, 1174–1179.
- Poulin, R. 1999 The intra- and interspecific relationships between abundance and distribution of helminth parasites of birds. *J. Anim. Ecol.* **68**, 719–725.
- Purvis, A. & Rambaut, A. 1995 Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comput. Appl. Biosci.* **11**, 247–251.
- Purvis, A., Gittleman, J. L. & Luh, H.-K. 1994 Truth or consequences: effects of phylogenetic accuracy on two comparative methods. *J. Theor. Biol.* **167**, 293–300.
- Ruokonen, M., Kvist, L. & Lumme, J. 2000 Close relatedness between mitochondrial DNA from seven *Anser* goose species. *J. Evol. Biol.* **13**, 532–540.
- Saunders, M. A. & Edwards, S. V. 2000 Dynamics and phylogenetic implications of mtDNA control region sequences in New World jays (Aves: Corvidae). *J. Mol. Evol.* **51**, 97–109.
- Sheldon, F. H., McCracken, K. G. & Stuebing, K. D. 1995 Phylogenetic relationships of the zigzag heron (*Zebilus undulatus*) and white-crested bittern (*Tigriornis leucolophus*) estimated by DNA–DNA hybridization. *Auk* **112**, 672–679.
- Sheldon, F. H., Jones, C. E. & McCracken, K. G. 2000 Relative patterns and rates of evolution in heron nuclear and mitochondrial DNA. *Mol. Biol. Evol.* **17**, 437–450.
- Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and the classification of birds: a study in molecular evolution*. New Haven, CT: Yale University Press.
- Siegel-Causey, D. 1997 Phylogeny of the Pelecaniformes: molecular systematics of a privative group. In *Avian molecular*

- evolution and systematics* (ed. D. P. Mindell), pp. 159–171. San Diego, CA: Academic Press.
- Sinclair, I., Hockey, P., Hayman, P. & Arlott, N. 1996 *The larger illustrated guide to birds of southern Africa*. Cape Town: Struik.
- Slater, P., Slater, P. & Slater, R. 1989 *The Slater field guide to Australian birds*. The Rocks, NSW, Australia: Lansdowne.
- Swinton, W. E. 1965 *Fossil birds*, 2nd edn. London: British Museum.
- Swofford, D. L. & Maddison, W. P. 1987 Reconstructing ancestral character states under Wagner parsimony. *Math. Biosci.* **87**, 199–229.
- Systat 1997 *SYSTAT for windows, statistics, version 7 edn*. Evanston, IL: SYSTAT.
- Tanaka, Y. 1996 Social selection and the evolution of animal signals. *Evolution* **50**, 512–523.
- Trail, P. W. 1990 Why should lek-breeders be monomorphic? *Evolution* **44**, 1837–1852.
- Van Tyne, J. & Berger, A. J. 1976 *Fundamentals of ornithology*. New York: Wiley.
- Whitfield, D. P. 1987 Plumage variability, status signalling and individual recognition in avian flocks. *Trends Ecol. Evol.* **2**, 13–18.
- Wiens, J. J. 2001 Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends Ecol. Evol.* **16**, 517–523.
- Zahavi, A. 1975 Mate selection—a selection for a handicap. *J. Theor. Biol.* **53**, 205–214.
- Zar, J. H. 1999 *Biostatistical analysis*, 4th edn. Englewood Cliffs, NJ: Prentice-Hall.

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.

Visit <http://www.pubs.royalsoc.ac.uk> to see an electronic appendix to this paper.