



Research article

Components of phenotypic variation in avian ornamental and non-ornamental feathers

JOSÉ JAVIER CUERVO^{1,*} and ANDERS PAPE MØLLER²

¹*Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Calle General Segura 1, E-04001 Almería, Spain;* ²*Laboratoire d'Ecologie Evolutive Parasitaire, CNRS FRE 2365, Université Pierre et Marie Curie, 7 quai St. Bernard, Case 237, F-75252 Paris Cedex 05, France*

(*author for correspondence, tel.: +34-950-281045; fax: +34-950-277100;
e-mail: jcuervo@eeza.csic.es)

Received 31 July 2000; accepted 6 July 2001

Co-ordinating editor: P. Harvey

Abstract. Phenotypic variation, measured as the coefficient of variation (CV), is usually larger in secondary sexual characters than in ordinary morphological traits. We tested if intraspecific differences in the CV between ornamental and non-ornamental feather traits in 67 evolutionary events of feather ornamentation in birds were due to differences in (1) the allometric pattern (slope of the regression line when regressing trait size on an indicator of body size), or (2) the dispersion of observations around the regression line. We found that only dispersion of observations around the regression line contributed significantly to total variation. A large dispersion of observations around the regression line for ornamental feathers is consistent with these characters showing condition-dependence, supporting indicator models of sexual selection more strongly than a pure Fisher process. Ornamental feathers in males demonstrated negative allometry when regressed on tarsus length, which is a measure of skeletal body size. This finding is consistent with ornamental feather traits being subject to directional selection due to female mate preferences, where large body size is less important than in male–male competition. This pattern of phenotypic variation for avian secondary sexual characters contrasts with patterns of variation for insect genitalia, supposedly subject to sexual selection, since the latter traits only differ from ordinary morphology traits in allometry coefficient. The prevailing regime of selection (directional or stabilizing) and the effects of environmental factors are proposed to account for these differences among traits.

Key words: allometry, condition-dependence, feather ornaments, handicap, phenotypic variation, sexual selection

Introduction

Ornamental feathers in birds are secondary sexual characters presumed to have arisen and be maintained by sexual selection, mainly through mate choice. A number of different theories have been put forward to explain the evolution and the maintenance of costly ornamentation, and these include the Fisherian mechanism of arbitrary traits, the handicap mechanism, the sensory exploitation mechanism and several others (Andersson, 1994). Current empirical

evidence suggests that secondary sexual characters often demonstrate condition-dependent expression with huge variation in trait size, and only individuals in prime condition developing the most exaggerated secondary sexual characters (Andersson, 1994).

Population genetics theory suggests that underlying genetic variation in traits subject to strong directional selection as in sexually selected traits should be rapidly diminished (Borgia, 1979; Taylor and Williams, 1982; Falconer, 1989). However, there is little empirical evidence of lack of genetic variation in such traits (Hedrick, 1988; Pomiankowski and Møller, 1995). One explanation for this variability is that long-term directional selection may produce an increase in both the number of genes and the average effect of each locus on the trait (Pomiankowski and Møller, 1995). Greater than linear directional selection would select for greater phenotypic variation, while long-term stabilizing selection (as in most ordinary morphological traits) would cause the opposite effect. Thus, a large number of pathways contribute to the development of secondary sexual characters, and genetic variability in all of these different pathways will independently contribute to the expression of the sex trait (Rowe and Houle, 1996). If sexual traits are condition-dependent, and condition shows high genetic variance, high genetic variability of sexual traits could be explained by a large proportion of genetic variance in condition being captured and expressed by the trait (Kotiaho *et al.*, 2001).

Empirical tests have demonstrated that phenotypic variation in sexually selected feather traits, measured as the coefficient of variation (CV), is higher than in non-sexual characters of the same individuals (Alatalo *et al.*, 1988; Møller and Höglund, 1991; Møller and Pomiankowski, 1993a; Pomiankowski and Møller, 1995; Cuervo and Møller, 1999). Furthermore, an extensive comparative study of all 30 species for which genetic and phenotypic information is available has demonstrated that the phenotypic CV is strongly positively correlated with the additive genetic and the residual coefficient of variation in secondary sexual characters (Pomiankowski and Møller, 1995). Hence, we can hypothesize that traits with a high degree of phenotypic variation also have a high degree of genetic variation.

The use of the CV as a measure of the total amount of variation in the size of a morphological trait is not completely appropriate, because the CV is influenced by two different factors, as recently emphasized by Eberhard *et al.* (1998). If we regress the size of a morphological trait on an indicator of body size, for a given mean size we could obtain high levels of standard deviation either by large slopes or by large dispersion of points around the regression line (Fig. 1 in Eberhard *et al.* (1998)). It is crucial to distinguish between these two factors to understand the type of selection acting on specific morphological traits, because they arise from different mechanisms. On the one hand, positive allometries are supposed to indicate that sexual selection has played a role in

the evolution of the character through male–male competition (Simmons and Scheepers, 1996; Simmons and Tomkins, 1996). On the other, the degree of dispersion of points around the regression line may be related to various causes, as for example variation in developmental instability, genetic differences, and variation in environmental factors (Eberhard *et al.*, 1998).

For a large number of independent evolutionary events of feather ornaments in birds we have previously shown that ornaments differed from ordinary morphological traits in the same individuals by showing a larger CV (Cuervo and Møller, 1999). It has been hypothesized that secondary sexual characters have been subject to a recent history of intense directional selection (review in Andersson (1994)), while ordinary morphological traits have generally been subject to a much stronger component of stabilizing selection. Hence, the mode of selection (or a closely associated factor) would be responsible for the difference in CV. Another hypothesis would explain the difference in CV in terms of intensity of selection instead of mode of selection. According to standard evolutionary theory the genetic variation in a trait is maintained by a balance between selective loss and the generation of variability by mutation (Bulmer, 1980). The loss of variation would be proportional to the intensity of selection and, consequently, a more variable trait would be the one subject to less selection pressure. Therefore, ornamental feathers might show more variability than ordinary morphological traits if selection became weaker as the ornamental trait became exaggerated. However, this scenario is difficult to reconcile with the fact that the opposite trend is observed (Pomiankowski and Møller, 1995).

In this study we test for the relative importance of the two possible factors affecting CV (the slope of the regression line and the dispersion of observations around that line) in an attempt to elucidate the mechanisms responsible for the different patterns of variation in ornamental and non-ornamental feather traits. We contrast our findings for secondary sexual feather characters, supposedly subject to directional selection, as shown by several observational and experimental studies, with the results of a study of morphological variation in genitalia and other body parts of insects and spiders, recently published by Eberhard *et al.* (1998). Although Eberhard *et al.* (1998) have been criticized for their methods (Green, 1999), the main conclusions of their study seem to stand firm (Eberhard *et al.*, 1999).

Materials and methods

Definition of feather ornament

We studied 67 evolutionary events of exaggerated feather ornaments in birds using available phylogenetic information, following the criteria adopted by

Møller and Cuervo (1998) and Cuervo and Møller (1999). We did not consider sexually size monomorphic traits because there is only limited evidence for these being associated with sexual selection (review in Andersson (1994)). Sexually size dimorphic feather traits were considered to qualify as secondary sexual characters if there was a sex difference in their size of at least 5% because previous studies have considered this cut-off point for dimorphism (Höglund, 1989; Oakes, 1992; Höglund and Sillén-Tullberg, 1994). We have not included in the present study sexual differences in feather color or naked skin patches. If we suspected that a species might be sexually size dimorphic for a feather trait, we investigated this by measuring 10 adult males and 10 adult females of the species in question. A few species could not be measured due to a shortage of specimens in museum collections visited. A total of 82 species resulted in 12 being considered sexually size monomorphic and the remaining 70 being size dimorphic. We have not included three species (*Syrrhaptes paradoxus*, *Phaethornis superciliosus*, and *Lophornis ornata*) in our analyses because it was impossible to precisely measure tarsus length. Species with a feather character only being expressed in males were all included in the study. In two species (*Pteridophora alberti* and *Pavo cristatus*) only males were available. We have included female data in this study only when females were ornamented, that is, when female traits homologous to male feather ornaments were larger than expected for a particular feather tract.

Feather ornamentation has evolved a large number of times. If no other information was available, we assumed that there was only a single evolutionary event in each family. If ornaments appeared in subfamilies or tribes that were phylogenetically separated, these were considered to be independent evolutionary events. However, if for example an extravagant tail had evolved in one species and an extravagant head plume had evolved in another species of the same family, we assumed that they represented two different evolutionary events, since these traits were obviously developmentally and morphologically independent. For example, we considered seven different types of ornamental feathers in the tribe Paradisaeni, four in the subfamily Trochilinae, four in Phasianinae, etc. If more than a single ornamented species occurred within a taxon, we exclusively used abundance as the criterion for choice of a species due to more museum specimens being available for abundant species.

We used the phylogeny of Sibley and Ahlquist (1990), based on DNA–DNA hybridization, to identify different evolutionary events of extravagant feather ornamentation. For the family Hirundinidae, we used the phylogeny of Sheldon and Winkler (1993).

Data collection

For each species we measured 10 adults of each sex in major museum collections (see Acknowledgements), although it was impossible to obtain this number

of specimens in some cases. Specimens were chosen in the order in which they appeared in the collections, thereby preventing any involuntary bias in sampling. We only included adult specimens in breeding plumage and good feather condition. Individuals with broken or worn feathers were excluded. We were especially careful excluding specimens in molt by checking for the presence of feather quills. All specimens of each species belonged to the same subspecies and, when possible, to the same population. In *Hydrophasianus chirurgus* females were more ornamented than males apparently due to their polyandrous mating system, and females were thus used as the ornamented sex in the comparative analyses. Anyhow, qualitatively similar results are obtained if this species is not included in the analyses.

We measured the length of the left and the right character of the ornament (with a ruler to the nearest mm; usually elongated tail feathers or crests, but sometimes elongated feathers in wings and other feathers tracts), flattened wing (with a ruler to the nearest mm), tail (with a ruler to the nearest mm), and tarsus (with a digital caliper to the nearest 0.01 mm) according to Svensson (1984). Tail length was only used as a character in species where tail feathers were not a secondary sexual character. The size of characters was defined as the mean of the left and the right character value. Female traits homologous to male ornaments have been termed female ornaments, although this does not imply that these female traits are real ornaments. All species included in this study, their linear measurements, and the CV can be found in the Appendix of Cuervo and Møller (1999).

Statistical analyses

Tarsus length was chosen as an indicator of overall body size. We used ordinary least squares (OLS) regression of \log_{10} -transformed data to quantify the relationships between several morphological traits (wings, tails, ornaments) and tarsus length for each species and sex. The first independent aspect of the relationship between different parts of an animal's body is the dispersion of observations around the regression line. As an indicator of dispersion, we calculated the standard error of the estimate (SEE, the square root of the residual mean square from the regression line). This statistic gives an overall indication of the accuracy with which the fitted regression function predicts the dependence of Y on X (Zar, 1984, p. 271). Despite SEE not being dimensionless, the possible alternatives to express the dispersion of points around the regression line are less satisfactory. For example CV' , the coefficient of variation that Y would have if X were held constant, is a function of r , the square-root of the coefficient of determination ($CV' = CV(y) \times (1 - r^2)^{0.5}$), what implies that CV' can be calculated only when r is significant (see Eberhard *et al.* (1998)). Unfortunately, in our study only

37 out of 314 r -values are significant ($p < 0.5$), what precludes the use of CV'.

The second component of morphological variation is described by the slope of such regressions. The regression slopes of \log_{10} -transformed data are unaffected by the units of measurements of different structures (Smith, 1980), and they are commonly used in studies of allometry (Gould, 1966). Our analyses do not imply that one variable is dependent on another. However, the regressions provide a means to quantify and compare differences between the relationships of different variables with a common reference variable (the indicator of body size). Since we have made comparisons within species, we can consider each comparison as a statistically independent observation without the risk of introducing bias due to common ancestry.

OLS regressions assume that the independent variable is measured without error (Sokal and Rohlf, 1981, p. 459). Clearly, our data do not fit this assumption, since tarsus length is subject to measurement error. However, this inconvenience has been partly overcome in this study, because all regressions have tarsus as the independent variable. The effect of error in the independent variable should be cancelled out by pairwise comparisons of slopes. Since OLS regressions underestimate the slope of Y on X as the amount of error in X increases (see references in Green (1999)), we should be cautious when considering the slope values themselves. However, we can be confident with the results when comparing slopes calculated with the same independent variable. The use of model II regression methods, for example reduced major axis (RMA) regressions, would be more problematic. The slope of RMA regressions is calculated by dividing the slope from OLS regressions by r -values. As already stated, most r -values in our study were not significant, and RMA slopes calculated with non-significant r -values would then be meaningless. Therefore, we have decided to use slopes from OLS regressions throughout. Standard errors of estimates and slopes from OLS regressions for each species and sex can be found in the Appendix.

Repeatabilities of the linear measurements in four species with different kinds of ornaments and different body sizes (Becker, 1984) were large (Cuervo and Møller, 1999), suggesting that our measurements were sufficiently precise to allow quantitative analyses, without any indication that small species had larger measurement errors than large species. We assessed the repeatabilities by measuring the same individuals on two different days without knowledge of the results obtained on the first day. We have also calculated in the same four species the CV of first and second measurements for the statistics used in this study (calculations are based on \log_{10} -transformed data). Variation in SEE was 0.0% for wing feathers, 0.0–2.9% for tails, and 0.9–3.1% for ornamental feathers. Variation in slope was 3.5–6.3% for wing feathers, 2.5–8.8% for tails, and 0.5–5.7% for ornamental feathers.

Results

The null hypothesis predicts no significant difference in the standard error of the estimate of the regression (SEE) between secondary sexual characters and ordinary morphological traits when regressed on a measure of structural body size (tarsus length in the present study). The dispersion of observations around the allometric line (as measured by SEE) was significantly larger for ornaments than for non-ornamental traits (wing, tail) in both males and females (Table 1).

The second factor affecting the CV is the allometry coefficient or slope of the regression line. The larger the value of the slope, the stronger its contribution to total variation. The slopes of ornamental and non-ornamental feather traits in both males and females were not significantly different (Table 1). Slopes for ornaments and for wing feathers were quite different in females (Table 1), but the difference was no longer significant after sequential Bonferroni-adjustment (Rice, 1989).

The previous analyses were based on ornamental feathers of different types and sizes. Most ornamental feathers could be grouped as elongated rectrices (including both central and outermost tail feathers) and head or neck feathers (crests, ears, moustaches, head plumes, neck tufts), the latter much shorter than the former in both sexes (t -tests on \log_{10} -transformed values, $t \geq 8.88$, $df \geq 41$, $p < 0.001$). Ornamental head feathers were significantly shorter than non-ornamental feathers (wings, ordinary tails) in both sexes (paired t -test, $t \geq 5.37$, $df \geq 15$, $p < 0.001$). However, ornamental rectrices were longer than wings in males ($t = -4.00$, $df = 31$, $p < 0.001$), and they did not differ significantly in size in females ($t = -0.41$, $df = 25$, $p = 0.68$). Since the difference in relative size between types of ornamental feathers could affect our analyses, we

Table 1. Comparison of slopes and SEE from ordinary least squares regressions between ornamental and non-ornamental feather traits. Female ornaments are simply female characters homologous to male ornaments, with no assumption of their function. Calculations are based on \log_{10} -transformed data

Statistic	Sex	Non-ornament mean (SE)	Ornament mean (SE)	n	Paired t	p
SEE	Male	Wing 0.011 (0.0005)	0.040 (0.002)	67	-16.39	<0.001
		Tail 0.021 (0.002)	0.039 (0.003)	31	-6.95	<0.001
	Female	Wing 0.013 (0.0006)	0.048 (0.004)	47	-8.77	<0.001
		Tail 0.018 (0.001)	0.056 (0.008)	21	-4.69	<0.001
Slope	Male	Wing 0.234 (0.047)	0.281 (0.174)	67	-0.31	0.76
		Tail 0.123 (0.118)	0.205 (0.162)	31	-0.44	0.67
	Female	Wing 0.201 (0.050)	-0.425 (0.314)	47	2.10	0.041
		Tail 0.156 (0.091)	-0.788 (0.639)	21	1.56	0.13

Table 2. Comparison of slopes and SEE from ordinary least squares regressions between ornamental and non-ornamental traits in birds with two kinds of ornamental feathers: elongated rectrices (T) and head and neck feathers (H). Calculations are based on \log_{10} -transformed data

Statistic	Sex	Comparison	df		Paired <i>t</i>		<i>p</i>	
			H	T	H	T	H	T
SEE	Male	Wing-ornament	24	31	-10.39	-11.67	<0.001	<0.001
		Tail-ornament	22	-	-7.02	-	<0.001	-
	Female	Wing-ornament	16	25	-5.40	-9.94	<0.001	<0.001
		Tail-ornament	15	-	-4.39	-	<0.001	-
Slope	Male	Wing-ornament	24	31	-0.10	-0.25	0.92	0.80
		Tail-ornament	22	-	-0.04	-	0.97	-
	Female	Wing-ornament	16	25	1.18	1.99	0.25	0.057
		Tail-ornament	15	-	1.04	-	0.31	-

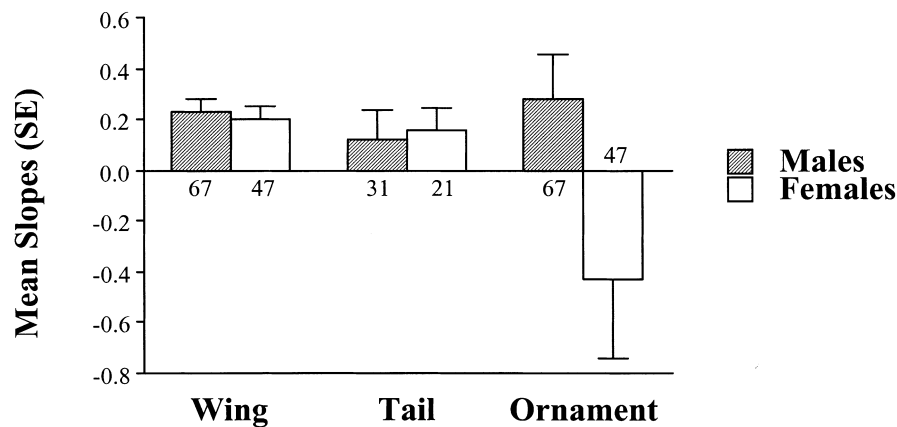


Figure 1. Mean (SE) slopes after regressing ornamental and non-ornamental (wing, tail) feather traits on an indicator of body size (tarsus) using ordinary least squares regression. Sample size (number of species) is indicated. Female characters homologous to male ornaments are termed female ornaments. All mean values are significantly different from one, but only slopes for wings in both sexes are significantly different from zero (one sample *t*-tests).

repeated the tests separately for species with elongated rectrices and ornamental head or neck feathers. However, the results were very similar for both categories of traits (Table 2).

Figure 1 shows mean slopes for ornamental and non-ornamental feather traits. All mean slopes were significantly smaller than one, demonstrating negative allometry (< 1), but only slopes for wings in both sexes were significantly different from zero (Fig. 1).

Discussion

Allometry

Regarding allometric pattern, we found no significant differences between the slopes for regressions of the size of ornamental and non-ornamental feather traits on a measure of skeletal body size. This result contrasts with previous studies comparing the slope of sexually and non-sexually selected traits. Eberhard *et al.* (1998) found that the allometric values of genitalic structures of insects and spiders were usually lower than those of other body parts in the same species. Female insects perceive male genitalia by touching these structures, while birds perceive ornamental feathers at a distance using vision. Therefore, in the context of tactile perception, female size is likely to affect perception of the male, and there will be selection on males to adjust their genitalia to that appropriate for the most typical female size. In other words, standard sizes and thus low allometric values will evolve due to stabilizing selection. This stabilizing selection will probably be stronger than the one affecting ordinary morphological traits. However, female size will be of much less importance in the perception of bird ornamental feathers, favoring selection for the most exaggerated male traits. Thus, directional selection will be more important and stabilizing selection less important for feather ornaments compared to insect genitalia, and feather ornaments will accordingly not show such a low allometric pattern.

Since different kinds of ornaments may impose different costs on their bearers, a distinction between categories of ornaments may be of vital importance in order to understand their allometric patterns. Therefore, we have re-analyzed separately two broad categories of traits. Elongated rectrices have a function in terms of sexual attractiveness, but they also affect flight performance. Ornamental feathers on head and neck are relatively small compared to rectrices, and they may therefore impose relatively minor aerodynamic costs. However, we found similar allometric patterns for the two categories of traits (Table 2), despite striking differences in relative size of these two kinds of ornaments. This implies that the similarity in slope (and the differences in SEE) we have found between ornamental and non-ornamental feathers are not particularly influenced by the size of the ornament. The lack of difference between the two types of ornamental feathers may be explained if both are subject to similar selection pressures despite differences in size. This would be possible because ornaments are integrated into the entire Bauplan of an individual due to selection pressures on non-ornamental morphology to reduce costs of ornamentation. There is comparative evidence and evidence from studies of single species suggesting that the entire phenotype of an ornamented species is shaped during the course of evolution to reduce the costs of the ornament (Balmford *et al.*, 1994; Møller, 1996).

Figure 1 shows that the mean slope for ornamental feathers in males (the trait expected to be maintained by directional sexual selection), ornamental feathers in females (female traits homologous to male ornaments), and ordinary tail feathers in both sexes do not differ significantly from zero. This result suggests that the length of ornamental and tail feathers is not related to skeletal body size. On the contrary, wing size shows a significant relationship with tarsus length, although with negative allometry (<1).

Previous studies on ornamental traits in a small number of bird species (Petrie, 1988, 1992; Alatalo *et al.*, 1988; Møller, 1991; Green, 1992) have shown that allometry in ornaments is usually positive (>1). However, the present study based on a much larger sample size shows that positive allometry is uncommon for ornamental feathers. Positive allometry can be explained by differential costs and benefits of ornamental feathers in relation to body size (Petrie, 1992). When a character functions to display competitive ability (for example through male–male competition), positive allometry can arise from smaller costs and larger benefits for individuals of large body size and hence superior competitive ability (Petrie, 1988). When a character has evolved due to mate choice, the relationship between the relative costs and benefits of the character and body size is less obvious. In other words, while mate choice does not predict positive allometry, male–male competition does. Therefore, our finding of negative slopes for extravagant feather ornaments is consistent with attraction of mates being the most important function of these ornamental characters, as suggested by the extensive empirical evidence (Andersson, 1994). Although we cannot exclude the possibility that females prefer large feather ornaments in order to mate with large males, our results allow us to suggest that this possibility is less likely for ornamental feathers than for other sexually selected traits.

We should have in mind that OLS regressions underestimate the slope of Y on X as the amount of error in X increases, so we must be cautious when interpreting the slope values found in this study. However, we can be confident that comparisons of slopes calculated from regressions with the same independent variable are unaffected by this problem.

Dispersion of points around the regression line

Regarding the dispersion of points around the regression line, we found on average a larger dispersion for ornaments than for non-ornamental traits. This result may be related to variation in developmental instability, genetic differences, and/or variation in environmental factors. A previous study of the species included here (Cuervo and Møller, 1999) have shown that fluctuating asymmetry (a measure of developmental instability) in ornaments was significantly larger than in non-ornaments. This difference between kinds of traits has also been found in other studies (Møller, 1990, 1992a, b; Møller and Höglund, 1991; Møller

Pomiankowski, 1993a), suggesting that ornaments are more susceptible to disruption of developmental homeostasis than ordinary morphological traits (Møller and Pomiankowski, 1993b). The different prevailing selection regimes affecting the two kinds of traits may account for this difference. However, we have reduced any effect of differences due to developmental instability because the size of each trait was defined as the mean of the left and the right character.

We have attempted to remove inter-population genetic variability by choosing individuals from the same subspecies and, when possible, individuals from the same population. However, we cannot discard the possibility that some variation persists, although this variation should not significantly affect our conclusions.

Differences between ornamental and non-ornamental feather characters in the dispersion of points around the regression line still persist after minimizing the effect of developmental instability and genetic differences. Hence, we suggest that differences in dispersion of points are due to variation in environmental factors, they may affect the expression of ornaments more strongly than the expression of non-ornamental traits. For example, resource availability and/or parasite infections may directly affect body condition, at least during the period of feather growth. If the development of a secondary sexual trait reflects the overall condition of its bearer, such ornaments will be condition-dependent handicaps (Zahavi, 1975, 1977; Andersson, 1982, 1986a, b; Dominey, 1983; Kodric-Brown and Brown, 1984; Nur and Hasson, 1984; Pomiankowski, 1987a, b; Michod and Hasson, 1990; Iwasa *et al.*, 1991). Ornamental feathers are presumably condition-dependent, and consequently, our results support indicator models of sexual selection for the evolution of ornamental feathers more strongly than a pure Fisher process. While indicator models predict condition-dependent expression of ornaments, the Fisher process predicts that ornaments should be arbitrary with respect to condition (Fisher, 1930; Lande, 1981; Kirkpatrick, 1982; Pomiankowski *et al.*, 1991). Price *et al.* (1993) predicted that a strong relationship between sexual characters and condition should be associated with high levels of variability of the sexual characters. Our results suggest that ornamental feathers are condition-dependent and we had also shown in a previous study (Cuervo and Møller, 1999) that ornamental feathers are more variable than non-ornamental characters. Therefore, our results are indeed in accordance with the predictions of Price *et al.* (1993). Eberhard *et al.* (1998) did not find significant differences in the dispersion of points around the allometric lines between genitalia and other morphological traits, possibly due to both types of characters being little affected by variation in environmental factors due to their lack of condition dependence.

In conclusion, feather ornaments demonstrated considerable phenotypic variation compared to non-ornamental traits in a comparative study of birds (Cuervo and Møller, 1999). This variation was mainly caused by variation in

the dispersion of observations around the regression line, but not by differences in allometry. This suggests that feather ornaments often are condition-dependent, supporting indicator-models of sexual selection for the evolution of ornamental feathers more strongly than a pure Fisher process. Our finding of ornamental feathers showing negative allometry when regressed on a measure of skeletal body size is consistent with these traits being subject to directional selection due to female mate preferences.

Acknowledgements

We are grateful to the curators of the bird collections in Alexander Koenig Museum, Bonn, Germany, British Museum (Natural History), Tring, UK, Doñana Biological Station, Seville, Spain, Natural History Museum, Stockholm, Sweden, and Zoological Museum, Copenhagen, Denmark, for access to specimens. A.J. Green kindly provided constructive criticism. J.J.C. was supported by a post-doctoral grant from the EU (Human Capital and Mobility Program) and by Spanish DGICYT (PB95-0110). A.P.M. was supported by an ATIPE BLANCHE from the CNRS.

Appendix

Slopes when ornamental and non-ornamental (wing, tail) feather traits are regressed on an indicator of body size (tarsus) using ordinary least squares regression. All variables have been \log_{10} -transformed before regressions. SEE = standard error of estimate; SE = standard error of the slope.

Species (kind of ornament)	Sex	<i>n</i>	Trait	SEE	Slope (SE)
<i>Podiceps cristatus</i> (ears)	Male	10	Wing	0.008	0.389 (0.139)
			Ornament	0.039	1.545 (0.682)
	Female	10	Wing	0.014	0.008 (0.246)
			Ornament	0.057	0.127 (1.016)
<i>Anas falcata</i> (wing feathers)	Male	10	Wing	0.009	0.231 (0.175)
			Tail	0.035	-0.598 (0.713)
			Ornament	0.026	0.164 (0.535)
	Female	10	Wing	0.006	0.343 (0.141)
			Tail	0.024	0.155 (0.570)
			Ornament	0.043	-1.883 (1.037)
<i>A. platyrhynchos</i> (central tail feathers)	Male	10	Wing	0.022	0.359 (0.433)
			Tail	0.017	-0.300 (0.340)
			Ornament	0.055	-0.207 (1.08)
<i>Aythya fuligula</i> (crest)	Male	10	Wing	0.011	0.196 (0.340)
			Tail	0.022	-0.557 (0.668)
			Ornament	0.067	0.651 (2.075)
	Female	10	Wing	0.010	-0.425 (0.477)
			Tail	0.017	-0.322 (0.834)
			Ornament	0.154	-12.309 (7.709)

Appendix: (continued)

<i>Clangula hyemalis</i> (central tail feathers)	Male	10	Wing	0.016	-0.078 (0.319)
			Ornament	0.058	0.410 (1.194)
<i>Tetrao tetrix</i> (external tail feathers)	Male	10	Wing	0.008	0.192 (0.156)
			Ornament	0.029	-0.818 (0.561)
<i>Lophortyx californica</i> (head plumes)	Female	10	Wing	0.018	0.043 (0.373)
			Ornament	0.035	-0.237 (0.709)
	Male	10	Wing	0.011	-0.056 (0.216)
			Tail	0.015	0.133 (0.286)
<i>Rollulus rouloul</i> (crest)	Female	10	Ornament	0.030	-0.554 (0.578)
			Wing	0.009	0.495 (0.314)
	Male	10	Tail	0.030	-0.237 (1.055)
			Ornament	0.054	0.147 (1.915)
<i>Gallus gallus</i> (neck feathers)	Male	10	Wing	0.015	0.460 (0.637)
			Tail	0.038	0.944 (1.563)
	Female	10	Ornament	0.064	-2.458 (2.636)
Wing			0.017	0.470 (0.281)	
Ornament			0.051	-0.476 (0.829)	
<i>Phasianus colchicus</i> (central tail feathers)	Male	10	Wing	0.013	0.121 (0.303)
			Tail	0.019	-0.146 (0.438)
	Female	10	Ornament	0.038	0.160 (0.848)
			Wing	0.015	0.239 (0.181)
<i>P. cristatus</i> (train)	Male	10	Ornament	0.044	-0.464 (0.539)
			Wing	0.011	0.491 (0.270)
	Female	10	Ornament	0.038	-1.116 (0.927)
Wing			0.008	0.202 (0.103)	
Tail			0.032	-0.118 (0.383)	
<i>Otis tarda</i> (moustache)	Male	10	Ornament	0.037	-0.018 (0.543)
			Wing	0.012	0.426 (0.128)
	Female	10	Tail	0.018	0.301 (0.186)
			Ornament	0.068	-0.770 (0.722)
<i>H. chirurgus</i> (central tail feathers)	Male	10	Wing	0.014	-0.090 (0.239)
			Tail	0.015	0.279 (0.260)
	Female	10	Ornament	0.136	-1.754 (2.290)
			Wing	0.018	0.434 (0.250)
<i>Vanellus vanellus</i> (crest)	Male	10	Ornament	0.047	0.468 (0.641)
			Wing	0.029	0.929 (0.287)
	Female	10	Ornament	0.076	1.883 (0.759)
			Wing	0.010	-0.315 (0.300)
<i>Philomachus pugnax</i> (neck tuft)	Male	10	Tail	0.022	-0.566 (0.697)
			Ornament	0.051	0.786 (1.594)
	Female	10	Wing	0.014	0.300 (0.366)
			Tail	0.018	-0.026 (0.480)
<i>Treron apicauda</i> (central tail feathers)	Male	10	Ornament	0.112	-1.361 (2.984)
			Wing	0.010	0.242 (0.347)
	Female	10	Tail	0.017	0.340 (0.575)
			Ornament	0.051	0.509 (1.739)
<i>Psittacula longicauda</i> (central tail feathers)	Male	10	Wing	0.011	0.444 (0.216)
			Ornament	0.018	-0.336 (0.344)
	Female	10	Wing	0.011	-0.001 (0.218)
Ornament			0.041	0.002 (0.787)	
<i>Psittacula longicauda</i> (central tail feathers)	Male	10	Wing	0.007	-0.027 (0.295)
			Ornament	0.020	0.043 (0.795)

Appendix: (continued)

	Female	10	Wing	0.014	0.279 (0.357)
			Ornament	0.072	-0.493 (1.899)
<i>Scotornis climacurus</i> (central tail feathers)	Male	10	Wing	0.012	0.175 (0.300)
			Ornament	0.049	0.304 (1.210)
	Female	10	Wing	0.014	0.132 (0.312)
			Ornament	0.040	0.785 (0.867)
<i>Macrodipteryx longipennis</i> (wing feathers)	Male	10	Wing	0.010	0.225 (0.263)
			Ornament	0.039	-1.104 (1.038)
<i>Hydropsalis brasiliانا</i> (external tail feathers)	Male	10	Wing	0.011	1.049 (0.172)
			Ornament	0.052	2.541 (0.790)
	Female	10	Wing	0.013	0.533 (0.215)
			Ornament	0.039	1.071 (0.655)
<i>Trochilus polytmus</i> (2nd external tail feathers)	Male	10	Wing	0.010	0.417 (0.172)
			Ornament	0.032	0.270 (0.568)
	Female	10	Wing	0.013	-0.277 (0.250)
			Ornament	0.034	-1.830 (0.678)
<i>Topaza pella</i> (breast feathers)	Male	10	Wing	0.010	-0.593 (0.523)
			Ornament	0.029	0.533 (1.446)
<i>Oxygogon guerinii</i> (crest)	Male	10	Wing	0.009	0.125 (0.230)
			Tail	0.013	0.486 (0.338)
			Ornament	0.044	0.858 (1.105)
<i>Agelaiocercus kingi</i> (external tail feathers)	Male	10	Wing	0.009	0.089 (0.303)
			Ornament	0.040	-0.016 (1.362)
	Female	10	Wing	0.015	0.096 (0.310)
			Ornament	0.025	-1.713 (0.528)
<i>Pharomachrus mocinno</i> (tail coverts)	Male	10	Wing	0.012	0.032 (0.112)
			Ornament	0.057	0.375 (0.538)
	Female	10	Wing	0.012	-0.859 (0.460)
			Ornament	0.035	0.742 (1.294)
<i>Tanysiptera galatea</i> (central tail feathers)	Male	10	Wing	0.011	-0.443 (0.586)
			Ornament	0.029	0.129 (1.604)
	Female	10	Wing	0.020	0.242 (0.935)
			Ornament	0.074	-4.332 (3.394)
<i>Coracias abyssinicus</i> (external tail feathers)	Male	10	Wing	0.008	0.109 (0.133)
			Tail	0.013	0.270 (0.236)
			Ornament	0.034	-0.321 (0.601)
	Female	10	Wing	0.015	0.221 (0.218)
			Tail	0.019	0.444 (0.271)
			Ornament	0.031	0.181 (0.431)
<i>Dinopium javanense</i> (crest)	Male	10	Wing	0.020	0.740 (0.468)
			Tail	0.023	1.011 (0.530)
			Ornament	0.023	0.730 (0.534)
	Female	10	Wing	0.014	0.425 (0.241)
			Tail	0.020	0.385 (0.353)
			Ornament	0.062	0.708 (1.109)
<i>Pithys albifrons</i> (crest)	Male	10	Wing	0.011	0.125 (0.192)
			Tail	0.023	1.538 (0.398)
			Ornament	0.065	1.863 (1.129)
	Female	10	Wing	0.011	0.609 (0.349)
			Tail	0.027	0.397 (0.814)
			Ornament	0.048	2.622 (1.473)

Appendix: (continued)

<i>Rupicola peruviana</i> (crest)	Male	10	Wing	0.009	0.010 (0.153)
			Tail	0.012	0.067 (0.213)
			Ornament	0.023	-1.195 (0.403)
	Female	10	Wing	0.011	0.370 (0.137)
			Tail	0.008	-0.015 (0.117)
			Ornament	0.064	-0.003 (0.832)
<i>Pipra cornuta</i> (crest)	Male	10	Wing	0.009	0.386 (0.342)
			Tail	0.013	0.391 (0.505)
			Ornament	0.030	0.086 (1.208)
<i>Chiroxiphia linearis</i> (central tail feathers)	Male	10	Wing	0.008	0.069 (0.090)
			Ornament	0.039	0.416 (0.443)
			Female	10	Wing
Tail	0.022	-0.249 (0.546)			
Ornament	0.042	-1.724 (1.029)			
<i>Tyrannus savana</i> (external tail feathers)	Male	10	Wing	0.017	0.403 (0.383)
			Ornament	0.062	1.480 (1.412)
			Female	10	Wing
Ornament	0.057	1.207 (1.543)			
<i>Anairetes reguloides</i> (crest)	Male	8			Wing
			Tail	0.055	1.326 (1.367)
			Ornament	0.062	1.111 (1.532)
	Female	7	Wing	0.014	0.045 (0.199)
			Tail	0.013	-0.171 (0.186)
			Ornament	0.061	-0.974 (0.874)
<i>Menura novaehollandiae</i> (central tail feathers)	Male	10	Wing	0.012	-0.162 (0.258)
			Ornament	0.059	-1.539 (1.301)
			Female	8	Wing
Ornament	0.025	0.369 (0.329)			
<i>Eremophila alpestris</i> (head plumes)	Male	10			Wing
			Tail	0.022	0.177 (0.430)
			Ornament	0.031	0.046 (0.596)
	Female	10	Wing	0.016	-0.008 (0.260)
			Tail	0.022	0.172 (0.354)
			Ornament	0.047	-0.288 (0.760)
<i>Hirundo rustica</i> (external tail feathers)	Male	10	Wing	0.013	0.441 (0.341)
			Ornament	0.025	1.131 (0.632)
			Female	10	Wing
Ornament	0.034	-0.642 (0.686)			
<i>H. semirufa</i> (external tail feathers)	Male	10			Wing
			Ornament	0.054	0.688 (1.104)
			Female	10	Wing
Ornament	0.040	-0.589 (0.738)			
<i>Psalidoprocne obscura</i> (external tail feathers)	Male	10			Wing
			Ornament	0.054	-0.370 (0.691)
			Female	9	Wing
Ornament	0.059	-0.353 (0.581)			
<i>Dryoscopus sabinii</i> (upper tail coverts)	Male	10			Wing
			Tail	0.014	0.043 (0.210)
			Ornament	0.021	0.035 (0.318)
	Female	10	Wing	0.013	0.248 (0.548)
			Tail	0.022	0.572 (0.924)

Appendix: (continued)

<i>Ptilononys caudatus</i> (central tail feathers)	Male	10	Ornament	0.026	-2.151 (1.111)
			Wing	0.009	0.037 (0.216)
	Female	7	Ornament	0.030	0.351 (0.722)
Wing			0.008	0.633 (0.442)	
<i>Phainopepla nitens</i> (crest)	Male	10	Ornament	0.022	0.886 (1.224)
			Wing	0.008	0.526 (0.148)
			Tail	0.014	0.267 (0.261)
	Female	10	Ornament	0.021	0.011 (0.399)
			Wing	0.019	0.454 (0.301)
<i>Copsychus malabaricus</i> (central tail feathers)	Male	10	Tail	0.020	0.768 (0.322)
			Ornament	0.033	0.509 (0.534)
			Wing	0.011	0.458 (0.324)
	Female	10	Ornament	0.052	-0.072 (1.459)
			Wing	0.020	0.501 (0.431)
<i>Panurus biarmicus</i> (moustache)	Male	10	Ornament	0.031	0.034 (0.655)
			Wing	0.011	-0.101 (0.265)
			Tail	0.025	0.137 (0.574)
	Female	10	Ornament	0.031	0.244 (0.711)
			Wing	0.005	0.326 (0.156)
<i>Orthotomus sutorius</i> (central tail feathers)	Male	10	Tail	0.013	-0.845 (0.390)
			Ornament	0.018	-2.077 (0.526)
			Wing	0.014	2.072 (1.064)
	Female	10	Ornament	0.068	9.011 (5.365)
			Wing	0.015	-0.108 (0.557)
<i>Malurus splendens</i> (moustache)	Male	10	Ornament	0.039	0.009 (1.431)
			Wing	0.007	0.102 (0.220)
			Tail	0.013	-0.207 (0.396)
<i>Terpsiphone viridis</i> (central tail feathers)	Male	10	Ornament	0.028	-0.483 (0.851)
			Wing	0.014	0.557 (0.197)
			Ornament	0.072	0.108 (1.040)
	Female	10	Wing	0.013	-0.169 (0.245)
			Ornament	0.051	-0.117 (0.948)
<i>Nectarinia johnstoni</i> (central tail feathers)	Male	10	Wing	0.016	0.773 (0.334)
			Ornament	0.062	0.348 (1.279)
<i>Anthochaera carunculata</i> (central tail feathers)	Male	10	Wing	0.015	0.797 (0.449)
			Ornament	0.034	0.493 (1.005)
			Wing	0.013	0.722 (0.292)
	Female	10	Ornament	0.021	0.502 (0.496)
			Wing	0.015	1.014 (0.408)
<i>Prothemadera novaeseelandiae</i> (neck feathers)	Male	10	Tail	0.019	1.217 (0.512)
			Ornament	0.037	1.233 (1.004)
			Wing	0.018	0.475 (0.192)
	Female	10	Tail	0.020	0.482 (0.215)
			Ornament	0.040	0.940 (0.431)
<i>Melophus lathami</i> (crest)	Male	10	Wing	0.008	0.174 (0.215)
			Tail	0.023	-0.357 (0.600)
			Ornament	0.029	0.219 (0.733)
	Female	10	Wing	0.012	0.436 (0.332)
			Tail	0.022	0.277 (0.606)
			Ornament	0.035	1.316 (0.987)

Appendix: (continued)

<i>Cardinalis cardinalis</i> (crest)	Male	10	Wing	0.014	0.434 (0.336)			
			Tail	0.025	0.117 (0.596)			
			Ornament	0.032	0.322 (0.771)			
	Female	10	Wing	0.012	-0.209 (0.342)			
			Tail	0.016	-0.064 (0.471)			
			Ornament	0.031	0.235 (0.884)			
<i>Quiscalus mexicanus</i> (central tail feathers)	Male	10	Wing	0.009	0.246 (0.109)			
			Ornament	0.031	0.132 (0.358)			
			Female	10	Wing	0.026	0.040 (0.404)	
	Female	10	Ornament	0.044	-0.230 (0.681)			
			<i>Erythrura prasina</i> (central tail feathers)	Male	10	Wing	0.005	0.096 (0.250)
						Ornament	0.031	-1.540 (1.448)
Female	10	Wing				0.007	0.107 (0.235)	
	Female	10	Ornament	0.042	0.770 (1.318)			
			<i>Vidua macroura</i> (central tail feathers)	Male	10	Wing	0.014	-0.280 (0.288)
						Ornament	0.034	-0.094 (0.687)
<i>Euplectes jacksoni</i> (central tail feathers)	Male	10				Wing	0.010	0.294 (0.259)
			Ornament	0.030	0.700 (0.764)			
			<i>Aplonis metallica</i> (central tail feathers)	Male	10	Wing	0.005	-0.174 (0.126)
Ornament	0.022	-0.384 (0.571)						
Female	10	Wing				0.012	0.474 (0.264)	
	Female	10	Ornament	0.028	0.281 (0.599)			
			<i>Sturnus unicolor</i> (throat feathers)	Male	10	Wing	0.005	0.128 (0.160)
						Tail	0.018	-0.340 (0.580)
Ornament	0.052	1.081 (1.700)						
	Female	10	Wing	0.007	0.360 (0.167)			
			Tail	0.011	0.920 (0.249)			
			Ornament	0.061	1.053 (1.424)			
<i>Dicrurus paradisaeus</i> (external tail feathers)	Male	10	Wing	0.017	-0.357 (0.306)			
			Ornament	0.033	-3.032 (0.595)			
				Female	10	Wing	0.015	-0.348 (0.196)
Ornament	0.041	-0.453 (0.536)						
<i>Amblyornis subalaris</i> (crest)	Male	10				Wing	0.008	-0.166 (0.162)
			Tail	0.012	-0.256 (0.235)			
			Ornament	0.032	-0.234 (0.625)			
<i>P. alberti</i> (eye feather)	Male	9	Wing	0.014	0.224 (0.460)			
			Tail	0.017	0.204 (0.534)			
			Ornament	0.049	-0.346 (1.598)			
<i>Ptiloris magnificus</i> (flank plumes)	Male	10	Wing	0.005	0.412 (0.416)			
			Tail	0.013	0.454 (0.357)			
			Ornament	0.025	1.980 (0.693)			
	Female	10	Wing	0.016	0.308 (0.261)			
			Tail	0.011	0.506 (0.184)			
			Ornament	0.043	0.097 (0.692)			
<i>Semioptera wallacei</i> (wing feathers)	Male	10	Wing	0.007	0.185 (0.249)			
			Tail	0.023	-1.104 (0.783)			
			Ornament	0.022	-0.658 (0.741)			
<i>Lophorina superba</i> (cape)	Male	10	Wing	0.008	0.238 (0.243)			
			Tail	0.008	0.210 (0.236)			
			Ornament	0.023	0.219 (0.658)			
<i>Diphylodes magnificus</i> (neck tuft)	Male	10	Wing	0.011	0.100 (0.592)			
			Tail	0.021	-1.419 (1.137)			

Appendix: (continued)

<i>Paradisaea rubra</i> (central tail feathers)	Male	10	Ornament	0.036	1.451 (1.962)
			Wing	0.006	0.561 (0.189)
<i>Parotia lawesii</i> (breast shield)	Male	10	Ornament	0.007	0.875 (0.226)
			Wing	0.015	0.018 (0.238)
			Ornament	0.024	0.332 (0.385)

References

- Alatalo, R.V., Höglund, J. and Lundberg, A. (1988) Patterns of variation in tail ornament size in birds. *Biol. J. Linn. Soc.* **34**, 363–374.
- Andersson, M. (1982) Sexual selection, natural selection and quality advertisement. *Biol. J. Linn. Soc.* **17**, 375–393.
- Andersson, M. (1986a) Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution* **40**, 804–816.
- Andersson, M. (1986b) Sexual selection and the importance of viability differences: a reply. *J. Theor. Biol.* **120**, 251–254.
- Andersson, M. (1994) *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Balmford, A., Jones, I.L. and Thomas, A.L.R. (1994) How to compensate for costly sexually selected tails: the origin of sexually dimorphic wings in long-tailed birds. *Evolution* **48**, 1062–1070.
- Becker, W.A. (1984) *Manual of Quantitative Genetics*. 4th edn. Academic Enterprises, Pullman, WA.
- Borgia, G. (1979) Sexual selection and the evolution of mating systems. In M.S. Blum and N.A. Blum (eds) *Sexual Selection and Reproductive Competition in Insects*. Academic Press, New York, NY. pp. 19–80.
- Bulmer, M.G. (1980) *The Mathematical Theory of Quantitative Genetics*. Oxford University Press, Oxford, UK.
- Cuervo, J.J. and Møller, A.P. (1999) Phenotypic variation and fluctuating asymmetry in sexually dimorphic feather ornaments in relation to sex and mating system. *Biol. J. Linn. Soc.* **68**, 505–529.
- Dominey, W.J. (1983) Sexual selection, additive genetic variance and the “phenotypic handicap”. *J. Theor. Biol.* **101**, 495–502.
- Eberhard, W.G., Huber, B.A., Rodríguez, R.L., Briceño, R.D., Salas, I. and Rodríguez, V. (1998) One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. *Evolution* **52**, 415–431.
- Eberhard, W.G., Huber, B.A. and Rodríguez, R.L. (1999) Don’t forget the biology: a reply to Green. *Evolution* **53**, 1624–1627.
- Falconer, D.S. (1989) *Introduction to Quantitative Genetics*. 3rd edn. Longman, New York, NY.
- Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford, UK.
- Gould, S.J. (1966) Allometry and size in ontogeny and phylogeny. *Biol. Rev. Camb. Philos. Soc.* **41**, 587–640.
- Green, A.J. (1992) Positive allometry is likely with mate choice, competitive display and other functions. *Anim. Behav.* **43**, 170–172.
- Green, A.J. (1999) Allometry of genitalia in insects and spiders: one size does not fit all. *Evolution* **53**, 1621–1624.
- Hedrick, A.V. (1988) Female choice and the heritability of attractive male traits: an empirical study. *Am. Nat.* **132**, 267–276.
- Höglund, J. (1989) Size and plumage dimorphism in lek-breeding birds: a comparative analysis. *Am. Nat.* **134**, 72–87.
- Höglund, J. and Sillén-Tullberg, B. (1994) Does lekking promote the evolution of male-biased size dimorphism in birds? On the use of comparative approaches. *Am. Nat.* **144**, 881–889.

- Iwasa, Y., Pomiankowski, A. and Nee, S. (1991) The evolution of costly mate preferences. II. "handicap principle". *Evolution* **45**, 1431–1442.
- Kirkpatrick, M. (1982) Sexual selection and the evolution of female choice. *Evolution* **36**, 1–12.
- Kodric-Brown, A. and Brown, J.H. (1984) Truth in advertising: the kinds of traits favored by sexual selection. *Am. Nat.* **124**, 309–323.
- Kotiaho, J.S., Simmons, L.W. and Tomkins, J.L. (2001) Towards a resolution of the lek paradox. *Nature* **410**, 684–686.
- Lande, R. (1981) Models of speciation by sexual selection on polygenic characters. *Proc. Natl. Acad. Sci. USA* **78**, 3721–3725.
- Michod, R.E. and Hasson, O. (1990) On the evolution of reliable indicators of fitness. *Am. Nat.* **135**, 788–808.
- Møller, A.P. (1990) Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim. Behav.* **40**, 1185–1187.
- Møller, A.P. (1991) Sexual selection in the monogamous barn swallow (*Hirundo rustica*). I. Determinants of tail ornaments size. *Evolution* **45**, 1823–1836.
- Møller, A.P. (1992a) Patterns of fluctuating asymmetry in weapons: evidence for reliable signalling of quality in beetle horns and bird spurs. *Proc. R. Soc. Lond. B* **248**, 199–206.
- Møller, A.P. (1992b) Parasites differentially increase the degree of fluctuating asymmetry in secondary sexual characters. *J. Evol. Biol.* **5**, 691–699.
- Møller, A.P. (1996) The cost of secondary sexual characters and the evolution of cost-reducing traits. *Ibis* **138**, 112–119.
- Møller, A.P. and Cuervo, J.J. (1998) Speciation and feather ornamentation in birds. *Evolution* **52**, 859–969.
- Møller, A.P. and Höglund, J. (1991) Patterns of fluctuating asymmetry in avian feather ornaments: implications for models of sexual selection. *Proc. R. Soc. Lond. B* **245**, 1–5.
- Møller, A.P. and Pomiankowski, A. (1993a) Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.* **32**, 167–176.
- Møller, A.P. and Pomiankowski, A. (1993b) Fluctuating asymmetry and sexual selection. *Genetica* **89**, 267–279.
- Nur, N. and Hasson, O. (1984) Phenotypic plasticity and the handicap principle. *J. Theor. Biol.* **110**, 275–297.
- Oakes, E.J. (1992) Lekking and the evolution of sexual dimorphism in birds: comparative approaches. *Am. Nat.* **140**, 665–684.
- Petrie, M. (1988) Intraspecific variation in structures that display competitive ability: large animals invest relatively more. *Anim. Behav.* **36**, 1174–1179.
- Petrie, M. (1992) Are all secondary sexual display structures positively allometric and, if so, why? *Anim. Behav.* **43**, 173–175.
- Pomiankowski, A. (1987a) The costs of choice in sexual selection. *J. Theor. Biol.* **128**, 195–218.
- Pomiankowski, A. (1987b) The "handicap" principle does work – sometimes. *Proc. R. Soc. Lond. B* **127**, 123–145.
- Pomiankowski, A., Iwasa, Y. and Nee, S. (1991) The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution* **45**, 1422–1430.
- Pomiankowski, A. and Møller, A.P. (1995) A resolution of the lek paradox. *Proc. R. Soc. Lond. B* **260**, 21–29.
- Price, T., Schluter, D. and Heckman, N. (1993) Sexual selection when the female directly benefits. *Biol. J. Linn. Soc.* **48**, 187–211.
- Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution* **43**, 223–225.
- Rowe, L. and Houle, D. (1996) The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond. B* **263**, 1415–1421.
- Sheldon, F.H. and Winkler, D.W. (1993) Intergeneric by phylogenetic relationships of swallows estimated by DNA–DNA hybridization. *Auk* **110**, 798–824.
- Sibley, C.G. and Ahlquist, J.E. (1990) *Phylogeny and Classification of Birds*. Yale University Press, New Haven, CT.

- Simmons, R.E. and Scheepers, L. (1996) Winning by a neck: sexual selection in the evolution of giraffe. *Am. Nat.* **148**, 771–786.
- Simmons, L.W. and Tomkins, J.L. (1996) Sexual selection and the allometry of earwig forceps. *Evol. Ecol.* **10**, 97–104.
- Smith, R.J. (1980) Rethinking allometry. *J. Theor. Biol.* **87**, 97–111.
- Sokal, R.R. and Rohlf, F.J. (1981) *Biometry*. 2nd edn. Freeman, New York, NY.
- Svensson, L. (1984) *Identification Guide to European Passerines*. 2nd edn. L. Svensson, Stockholm, Sweden.
- Taylor, P.D. and Williams, G.C. (1982) The lek paradox is not resolved. *Theor. Popul. Biol.* **22**, 392–409.
- Zahavi, A. (1975) Mate selection – a selection for a handicap. *J. Theor. Biol.* **53**, 205–214.
- Zahavi, A. (1977) The costs of honesty (further remarks on the handicap principle). *J. Theor. Biol.* **67**, 603–605.
- Zar, J.H. (1984) *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.