The allometric pattern of sexually size dimorphic feather ornaments and factors affecting allometry

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Abstract

The static allometry of secondary sexual characters is currently subject to debate. While some studies suggest an almost universal positive allometry for such traits, but isometry or negative allometry for nonornamental traits, other studies maintain that any kind of allometric pattern is possible. Therefore, we investigated the allometry of sexually size dimorphic feather ornaments in 67 species of birds. We also studied the allometry of female feathers homologous to male ornaments (female ornaments in the following) and ordinary nonsexual traits. Allometries were estimated as reduced major axis slopes of trait length on tarsus length. Ornamental feathers showed positive allometric slopes in both sexes, although that was not a peculiarity for ornamental feathers, because nonsexual tail feathers also showed positive allometry. Migration distance (in males) and relative size of the tail ornament (in females) tended to be negatively related to the allometric slope of tail feather ornaments, although these results were not conclusive. Finally, we found an association between mating system and allometry of tail feather ornaments, with species with more intense sexual selection showing a smaller degree of allometry of tail ornaments. This study is consistent with theoretical models that predict no specific kind of allometric pattern for sexual and nonsexual characters.

Introduction

For a long time it has been generally accepted that secondary sexual characters such as ornaments or weapons show positive allometry in relation to body size, i.e. large individuals have disproportionately larger secondary sexual characters than small individuals (Huxley, 1932; Green, 1992, 2000; Petrie, 1992; Kodric-Brown *et al.*, 2006). Here we refer to static allometry, defined as variation in the relative size of secondary sexual characters among individuals of the same species and developmental stage. The fundamental function of secondary sexual characters is to increase mating success, either by attracting mates (ornaments), by preventing competitors from having access to mates (weapons) or

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both. Such characters are generally assumed to be subject to intense directional selection and are often condition-dependent (Andersson, 1994). Therefore, the simplest explanation for positive allometry of these traits is that individuals achieve greater fitness benefits by increasing the size of secondary sexual characters than by increasing general body size, but only individuals in prime condition, i.e. the largest ones, will be able to develop large ornaments or weapons. In contrast, nonsexual traits are assumed to show negative allometry or isometry, i.e. they should grow relatively smaller with increasing body size or in proportion to body size. In fact, the kind of allometry shown by a trait (positive allometry, isometry or negative allometry) has been proposed to allow discrimination between sexual and nonsexual traits (Green, 2000).

Although certain types of secondary sexual characters indeed show positive allometry in some taxa (e.g. Kawano, 1997; Rosenberg, 2002), other authors have

cast doubt on the generality of this phenomenon. Bonduriansky (2007) recently argued that the apparent widespread positive allometry of secondary sexual characters was simply the result of biased sampling, with a clear preponderance of unusually exaggerated secondary sexual traits being included in allometry studies. In an attempt to correct for this bias, he reviewed allometric patterns in four groups of animals (birds, poeciliid fishes, flies and water striders) that have been subject to significant research on sexual selection, but have not been chosen for the conspicuousness of their ornaments or weapons. He found diverse allometric patterns for both sexual and nonsexual characters, including isometry and positive and negative allometry (Bonduriansky, 2007). These results suggest that the kind of trait (sexual vs. nonsexual) or even the mode of selection (directional vs. stabilizing) does not determine the kind of allometry. Consistent with these findings, theoretical models predict that sexual selection can lead to any type of allometric pattern, and not only to a positive one (Bonduriansky & Day, 2003). In fact, directional selection might result, at least theoretically, in any kind of allometry, from negative to positive, depending on the relative strength of selection for a particular trait at different body sizes (Eberhard et al., 2009).

One of the studies reviewed by Bonduriansky (2007) compared the allometries of ornamental and nonornamental feathers in 67 species of birds (Cuervo & Møller, 2001). That study found that both kinds of feathers showed negative allometries, i.e. large individuals exhibited relatively smaller ornaments (and also tail and wing feathers) than small individuals. Furthermore, ornamental and nonornamental feathers did not differ significantly in the degree of allometry. These results contradicted the traditional view that sexual ornaments almost universally showed positive allometry. However, allometric slopes had been calculated using ordinary least squares (OLS) regressions, and this type of regression assumes that the independent variable is measured without error; an assumption that was not met in the study (Cuervo & Møller, 2001). As already stated in the original paper and pointed out by Bonduriansky (2007), the slopes had been underestimated to some degree and should be considered with caution. Model II regressions, such as reduced major axis (RMA) regression, are more appropriate to quantify allometry (Green, 1999 and references therein).

The study of Cuervo & Møller (2001) is of special interest because it included an exhaustive investigation of patterns of allometry in a class of animals, the birds, thus excluding possibilities for biased sampling as a cause of the general patterns of allometry recorded. Here we report RMA instead of OLS slopes to provide more reliable estimates of allometry, allowing us to test in a more appropriate way the hypothesis that secondary sexual characters (feather ornaments in this case) ubiquitously show positive allometry. We also re-analysed the comparison between slopes of ornamental and nonornamental characters with the new RMA estimates. Cuervo & Møller (2001) regressed the size of both ornamental and nonornamental feather traits on tarsus length as an estimate of body size, and thus all OLS regressions for a particular species and sex had the same independent variable. This was interpreted as slopes being underestimated in a similar way, making the published comparison justified. However, the degree of underestimation in OLS regressions increases with scatter around the regression line (Bonduriansky, 2007). As shown by Cuervo & Møller (2001), dispersion of observations around the regression line was much larger for ornamental than for nonornamental feathers. Therefore, the comparison of OLS slopes might have been biased even when comparisons were made for each species and sex.

According to Bonduriansky (2007), we are still far from understanding the different factors that explain variability in allometric patterns in nature. Therefore, the aim of our study was to investigate predictors of allometry in our sample of ornamented bird species. Here we investigate the effect of relative size of the ornament, migration distance and mating system on the degree of allometry. First, Bonduriansky (2007) suggested that many allometry studies have found positive allometries because exaggerated secondary sexual traits were overrepresented, implying that the degree of allometry should be positively related to the relative size of the ornament. Here we provide a test of this prediction. Second, flight is an energetically very costly activity in birds, and the cost of having feather ornaments, which are aerodynamically nonfunctional (Balmford et al., 1993), should increase with migration distance between breeding areas and wintering grounds in migratory species. Thus, we tested the prediction of a negative relationship between degree of allometry and migration distance. Third, mating systems provide information about the intensity of sexual selection, because the most skewed mating success gives rise to the most intense selection. Theoretical models suggest that allometry reflects the relative fitness advantages that individuals differing in ornament size relative to body size acquire (Kodric-Brown et al., 2006). The mating advantages of relatively large ornament size, and thus the degree of allometry, should be greater when mating success among individuals is more skewed. However, we note that other models do not predict any particular relationship between allometry and intensity of selection (Bonduriansky & Day, 2003).

Materials and methods

Data collection

Most of the methods used in this study are explained in detail in Cuervo & Møller (2001), but we summarize the main points here. In brief, 67 bird species with

feather ornaments were studied, providing an exhaustive sample of evolutionary events of exaggerated feather characters in birds. A feather trait was considered to be an ornament, i.e. a secondary sexual character, when it was sexually size dimorphic and the mean sexual difference in size was at least 5%. The real function of presumed ornaments has not been studied in most avian species, but we assume that sexually size dimorphic feathers as defined above have been elongated in males owing to sexual selection (see numerous examples in Andersson, 1994). Other types of feather ornamentation (e.g. shape or colour) have not been considered in this study. Ten specimens for each species and sex were measured in museum collections (see Acknowledgments), although it was impossible to reach this sample size in some cases (mean sample size ± SE = 9.89 ± 0.05, range 7–10, $n = 114$). Although 10 specimens for each species and sex is a relatively small number, it was necessary to reach a compromise between the number of specimens per species and the number of species included in the study, because increasing the former would have decreased the latter, or would have caused sampling effort to differ greatly among species. Only adults in breeding plumage and good feather condition were included. We measured the length of the right and the left side of the following traits: wing, tail, ornament (all three with a ruler to the nearest mm) and tarsus (with a digital calliper to the nearest 0.1 mm). The size of a trait was calculated as the mean of the right and left side values. Tail length was only used as a trait when tail feathers were not secondary sexual characters. Female traits homologous to male ornaments were named female ornaments, although it does not imply any function, as probably they are not generally used to attract mates. We have included female data in this study only when female traits homologous to male feather ornaments were larger than expected for a particular feather tract. All species included in this study and the kind of ornament are reported in Cuervo & Møller (2001). All linear measurements (mean and SE) and sample sizes can be found in Cuervo & Møller (1999).

Migration distance was calculated as the distance, in latitudinal degrees, between the mid-points of the breeding and the winter ranges. These mid-points were simply the average of the northernmost and southernmost latitudes of the geographical distribution of the species during each period of the year. Geographical distributions were found in bird handbooks and field guides. Obviously, migration distance for all sedentary species was zero. Mating systems were categorized in three groups according to skew in male mating success: social monogamy (least skewed), polygyny and lekking (most skewed). Information on mating systems was obtained from Cuervo & Møller (1999), with the exception of *Sturnus unicolor* that we now consider polygynous instead of monogamous (Veiga *et al.*, 2001). *Hydrophasi-*

anus chirurgus has a polyandrous mating system and was included under the category polygyny. In this sex-role reversed species females are more ornamented than males, and female measurements were therefore used in the analyses as 'male measurements' and male measurements as 'female measurements'. Migration distance and mating system category for all species are shown in the Appendix.

Testing the possible relationships between allometry and other variables such as mating system requires comparisons among species, and the use of species-specific values as statistically independent observations might be incorrect if species share phenotypes due to common descent (Harvey & Pagel, 1991). We have thus controlled for similarity in allometry due to common phylogenetic descent in our analyses (see below). First, the phylogenetic relationships among species had to be determined. We followed the phylogenies by Sibley & Ahlquist (1990) for nonpasserines and suboscine passerines and by Barker *et al.* (2004) for oscine passerines. Other phylogenies were used for particular families: Phasianidae (Kolm *et al.*, 2007), Anatidae (Donne-Goussé *et al.*, 2002), Trochilidae (Altshuler *et al.*, 2004), Caprimulgidae (Larsen *et al.*, 2007), Paradisaeidae (Nunn & Cracraft, 1996), and Hirundinidae (Sheldon & Winkler, 1993). The position of the genera *Trochilus* and *Oxypogon* within Trochilidae as sister taxa of *Chlorostilbon* and *Metallura*, respectively, was determined according to Del Hoyo *et al.* (1999). In a similar way, the position of the genera *Semioptera* and *Pteridophora* within Paradisaeidae as sister taxa of *Paradisaea* and *Parotia*, respectively, was determined according to Frith & Beehler (1998). Our composite phylogeny is shown in Fig. 1.

Branch lengths from Sibley & Ahlquist (1990) were used when possible, but for portions of the phylogenetic tree extracted from other bibliographic sources (see above), the distance between species in the same genus were set to 1.1 $\Delta T_{50}H$ units, and between higher taxa to 3.4 $\Delta T_{50}H$ units (Sibley & Ahlquist, 1990; Bennett & Owens, 2002). Figure 1 shows branch lengths estimated in this way. This procedure actually implies an almost punctuational mode of evolution in the parts of the tree without branch length information, because all branches have the same length, except the two genera including more than one species (*Anas* and *Hirundo*). Therefore, we repeated the analyses assuming a gradual mode of evolution in the parts of the tree without branch length information. We used the algorithm from Grafen (1989) that assumes that branch lengths are related to the number of species in a clade. Both approaches provided qualitatively identical results with only one exception; the relationship between allometric slope and migration distance in males (see Results). In all other cases we have for brevity only shown results obtained with the first approach, i.e. with branch lengths shown in Fig. 1.
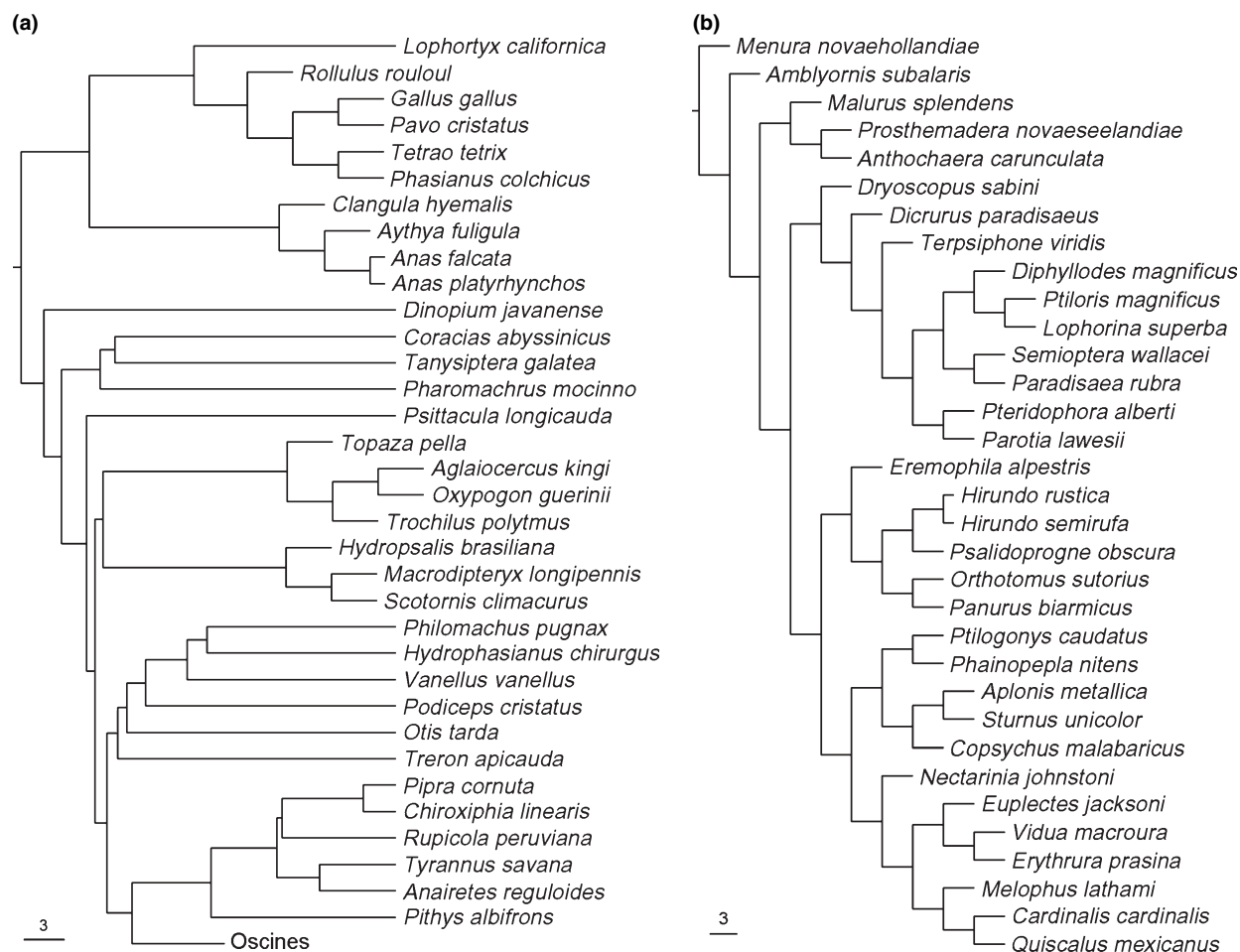
Fig. 1 Phylogeny of the 67 ornamented bird species included in this study. The branch length scale is given at the bottom left of each figure based on $\Delta T_{50}H$ units. $\Delta T_{50}H$ is a measure of the median sequence divergence of the genome and, thus, indicates phylogenetic distance between taxa. For bibliographic sources, see Materials and methods. (a) All bird species; (b) oscine passerines.

Although feather ornaments included in this study belonged to different feather tracts (Cuervo & Møller, 2001), most could be grouped as elongated rectrices (either central or outermost tail feathers) or head and neck feathers (crests, ears, moustaches, head plumes, neck tufts). Ornamental head and neck feathers were not only significantly shorter than ornamental tail feathers, but also shorter than nonornamental feathers (wings, ordinary tails) in both sexes (Cuervo & Møller, 2001). Ornamental tail feathers were longer than wings in males, but not in females (Cuervo & Møller, 2001). As these two types of ornamental feathers differed greatly in size, and because we predicted that relative size of ornaments would have an effect on allometry (see Introduction), we have repeated the statistical tests separately for these two groups of species. We have also compared allometric slopes between head/neck and tail feather ornaments. The kind of ornamental feather (head/neck feather, rectrice, other) for every species is shown in the Appendix.

Statistical analyses

The allometry of ornamental, wing and tail feathers can be estimated as the RMA slope after regressing feather trait length on an estimate of body size (tarsus length in our case). RMA slopes were calculated simply by dividing the standard deviation of $\log_{10}$-transformed feather trait length by the standard deviation of $\log_{10}$-transformed tarsus length (Bondurianský, 2007). The relative size of ornamental feathers was calculated as $\log_{10}$-transformed ornament length minus $\log_{10}$-transformed tarsus length. RMA slopes and the relative size of ornaments for every species and sex can be found in the Appendix. RMA slopes were $\log_{10}$-transformed to achieve normality (Kolmogorov–Smirnov test, $P > 0.20$ in all six cases) before further statistical analyses, although untransformed values were used when testing for differences in slopes from unity (Table 1). Migration distance could not be normalized because many species were sedentary

Table 1 Mean reduced major axis (RMA) slope of ornamental and nonornamental (wing, tail) feathers in relation to an estimate of body size (tarsus length) in 67 bird species.

Trait	Sex	RMA slope	SE	t	d.f.	P	r	CI lower	CI upper
Wing	Males	0.88	0.06	−1.98	66	0.052	0.237	−0.003	0.452
	Females	0.93	0.06	−1.29	46	0.20	0.187	−0.104	0.441
Tail	Males	1.59	0.17	3.54	30	0.0013	0.543	0.226	0.738
	Females	1.38	0.16	2.46	20	0.023	0.482	0.062	0.734
Ornament	Males	3.01	0.27	7.34	66	< 0.001	0.670	0.512	0.784
	Females	3.55	0.54	4.71	46	< 0.001	0.570	0.332	0.727
Ornamental tail	Males	3.13	0.50	4.28	31	< 0.001	0.609	0.321	0.777
	Females	2.79	0.37	4.79	25	< 0.001	0.692	0.404	0.837
Ornamental head	Males	3.24	0.33	6.71	24	< 0.001	0.808	0.590	0.901
	Females	4.79	1.36	2.79	16	0.013	0.572	0.120	0.801

Slopes of ornamental feathers were calculated for all species and also for two subgroups; species with ornamental tail feathers and species with ornamental head/neck feathers. Differences from unity for these mean slopes were tested using one-sample t-tests.

(thus having a migration distance of 0), but it was still Box-Cox transformed [$(\text{variable} + 0.1)^{0.3}$] before analyses in order to approach a normal distribution, because this is the most suitable transformation for normalizing skewed positive data containing zeros (Swaddle *et al.*, 1994). Mating system was included in the analyses as a ranked variable, and coded as 0 for social monogamy, 1 for polygyny and 2 for lekking.

Differences in allometry between ornamental and nonornamental feathers were tested within species, and, therefore, we consider each comparison a statistically independent observation without the risk of introducing bias due to similarity caused by common descent. However, differences in allometry between head/neck and tail feather ornaments and the possible relationship between allometry of ornaments and migration distance, mating system or relative size of ornaments were analysed across species, and phylogeny was taken into account in our analyses to control for possible phylogenetic effects (Harvey & Pagel, 1991). Similarity due to common phylogenetic descent was controlled by using the statistical software CAIC (Purvis & Rambaut, 1995) that calculates standardized contrasts between taxa for the variables of interest. To investigate the difference in allometry between head/neck and tail feather ornaments, we used the procedure Brunch of CAIC, and tested for differences from zero using one-sample t-tests on the mean contrasts. However, the relationship between the allometry of ornaments and other variables was investigated with the procedure Crunch of CAIC to calculate independent contrasts, and the variables were thus treated as continuous variables. The number of contrasts obtained with the procedure Crunch was the number of species minus 1. Subsequently, we analysed the contrasts using the Generalized Linear Model (GLZ) of the Statistica V8.0 software (StatSoft, Inc., 2007). GLZ was preferred over GLM because it is less restrictive regarding normality and homoscedasticity requirements. We considered the distribution of the dependent variable as normal and used the identity link function. The rela-

tionship between allometry of ornaments and any of the three variables was tested, while controlling for the effects of the other two. All regressions involving independent contrasts must pass through the origin (Purvis & Rambaut, 1995), and, therefore, GLZ analyses were performed with the intercept set to zero. All statistical tests were two-tailed.

In this study we performed multiple statistical tests, and it is well known that the risk of incurring Type I error increases with the number of tests performed. To alleviate this problem, we used sequential Bonferroni correction (Rice, 1989), but with a 10% level of significance to decrease the risk of incurring Type II error (Chandler, 1995). The number of tests included in the correction (k) is indicated in every case. However, Bonferroni correction has been severely criticized (e.g. Moran, 2003; Nakagawa, 2004), and some authors suggest, as an alternative, to show effect sizes and confidence intervals (CIs), because they allow us to evaluate the relative magnitude and hence the biological importance of the results (Nakagawa, 2004). Here we report standardized effect sizes (Pearson's r) and CIs for effect sizes for all statistical tests, in addition to exact P-values. Wald statistics (which are chi-squared distributed) and t statistics were transformed into r following Rosenthal (1994). CIs were calculated using the standard ($n > 50$) or the Hotelling ($n < 50$) z-transformation (Sokal & Rohlf, 1995, pp. 575–579). Effect sizes can be categorized as small ($r = 0.1$), medium ($r = 0.3$) or large ($r = 0.5$) according to Cohen (1988). Although there are no fixed rules, in general medium effect sizes can be considered biologically meaningful. For example, the average proportion of variance explained in ecological and evolutionary studies is no more than 7% (Møller & Jennions, 2002), that corresponds to an r-value of 0.265, slightly smaller than a medium effect size.

Results

The RMA slope of ornamental feathers in relation to an estimate of body size (tarsus length) was greater than one

in both sexes after sequential Bonferroni correction ($k = 10$), i.e. ornamental feathers showed positive allometry (Table 1). A qualitatively identical result was found when considering only species with tail ornamental feathers, only species with head/neck feather ornaments or all species (Table 1). As *Orthotomus sutorious* males and *Aythya fuligula* females showed extraordinarily large RMA slopes for ornamental feathers (tail ornamental feathers and crest feathers respectively; see Fig. 2 and the Appendix), we repeated the analyses excluding these two

particular cases, but the results, after sequential Bonferroni correction ($k = 10$), remained qualitatively identical. Regarding nonornamental feathers, the RMA slope of wing feathers was not significantly different from one in either sex, i.e. wing feathers showed isometry, but the RMA slope of nonornamental tail feathers was greater than one in both sexes after sequential Bonferroni correction ($k = 10$), thus implying positive allometry (Table 1). In some cases (wing feathers in *Orthotomus sutorius* males and *Tanysiptera galatea* females, tail feathers
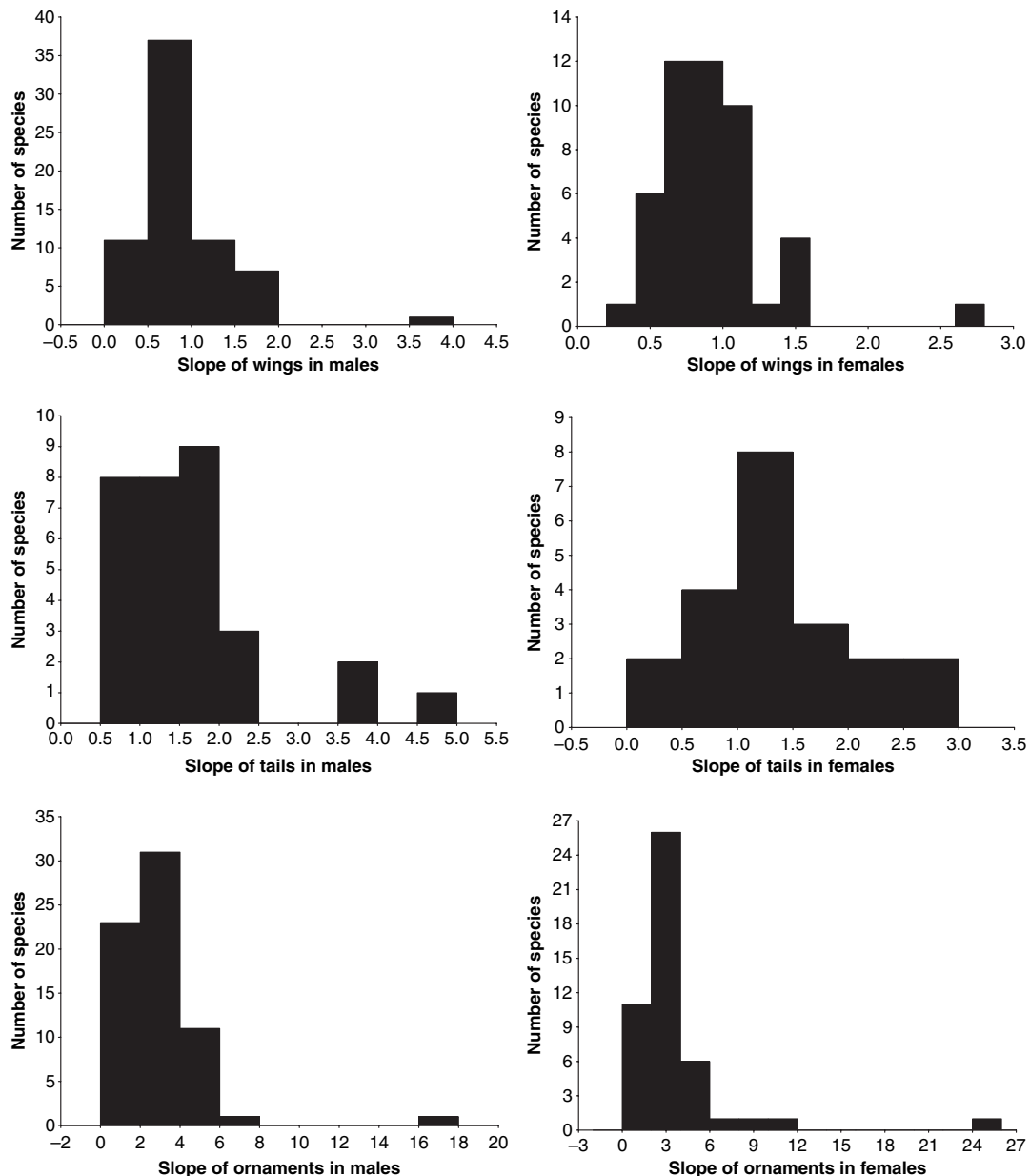

Fig. 2 Frequency distribution of reduced major axis slopes of wing, tail and ornamental feathers in male and female bird species. The database is available in the Appendix.

in *Diphyllodes magnificus* and *Rollulus rouloul* males), nonornamental characters also showed very large RMA slopes compared to the rest of the species (Fig. 2 and the Appendix). Even after excluding all these cases with presumably abnormal slopes from the analyses, the results were qualitatively identical, with the exception of wing feathers, which showed RMA slopes significantly smaller than one in both sexes after sequential Bonferroni correction ($k = 10$), i.e. wing feathers showed negative allometry (males: $t_{63} = -4.61$, $P < 0.001$, $r = 0.502$, CI lower = 0.292, CI upper = 0.666; females: $t_{44} = -2.90$, $P = 0.0059$, $r = 0.401$, CI lower = 0.119, CI upper = 0.611).

Within species, the RMA slope was significantly greater for ornamental than for nonornamental (wing, tail) feathers in both sexes after sequential Bonferroni correction ($k = 10$), and this result was consistent when considering only the subgroups of species with tail or head/neck ornaments (paired *t*-test, $15 \leq$ d.f. ≤ 66, $t \geq 6.76$, $P < 0.001$, $r \geq 0.833$ in all 10 tests). Results were qualitatively identical when cases with presumably abnormal slopes were excluded from the analyses. For males, the RMA slope of ornamental feathers was larger than the RMA slope of wing feathers in 67 of 67 species (100%), and larger than the RMA slope of nonornamental tail feathers in 28 of 31 species (90%), with exceptions being *Anas falcata*, *Dinopium javanense* and *Semioptera wallacei* (see the Appendix). For females, the RMA slope of ornamental feathers was larger than the RMA slope of wing feathers in 46 of 47 species (98%), with *Menura novaehollandiae* as the only exception, and larger than the RMA slope of nonornamental tail feathers in 21 of 21 species (100%) (see the Appendix). The RMA slope of head/neck feather ornaments did not differ significantly from the RMA slope of tail ornamental feathers either in males ($t_{20} = -0.54$, $P = 0.60$, $r = 0.120$, CI lower = -0.313, CI upper = 0.503) or in females ($t_{13} = -0.39$, $P = 0.71$, $r = 0.106$, CI lower = -0.456, CI upper = 0.597).

When considering all species together, the RMA slope of ornaments was not significantly related to migration distance, mating system or relative size of ornaments in either sex (n males = 66, n females = 46, $-0.11 \leq$ estimate ≤ 0.00, Wald $\chi_1^2 \leq 3.79$, $P \geq 0.052$, $r \leq 0.240$ in all six cases). A similar result was found when only species with ornamental head/neck feathers were included in the analyses (n males = 24, n females = 16, $-0.12 \leq$ estimate ≤ 0.10, Wald $\chi_1^2 \leq 1.09$, $P \geq 0.30$, $r \leq 0.262$ in all 6 cases). However, when only considering species with ornamental tail feathers, the RMA slope of ornaments was significantly negatively related to mating system in both sexes after sequential Bonferroni correction ($k = 6$) (Table 2, Fig. 3). The negative relationship between RMA slope and relative size of tail ornaments in females was marginally nonsignificant after sequential Bonferroni correction ($k = 6$) (Table 2). Although the relationships between the RMA slope and migration distance were not statistically significant, we suspected that the large number of sedentary species in our sample might have strongly affected these analyses. Therefore, the analyses were repeated excluding all sedentary species. Despite the dramatic reduction in sample size, the RMA slope of male ornaments was negatively related to migration distance after sequential Bonferroni correction ($k = 6$), when only species with ornamental tail feathers were considered ($n = 9$, estimate $\pm$ SE = -0.11 ± 0.04, Wald $\chi_1^2 = 9.58$, $P = 0.0020$, $r \approx 1$).

As stated above, *O. sutorious* males showed a very large RMA slope for ornamental tail feathers, and, thus, this extreme value might have a disproportionately strong influence on the relationship between the RMA slope of ornamental tails and mating system. However, when the independent contrasts of the RMA slopes of tail ornaments were ranked and the analyses repeated with these ranked values, the relationship with mating system was still significant in both sexes after sequential Bonferroni correction ($k = 6$) (males: $n = 31$, estimate $\pm$ SE = -30.16 ± 12.50, Wald $\chi_1^2 = 5.82$, $P = 0.016$, $r = 0.433$, CI lower = 0.091, CI upper = 0.668; females: $n = 25$, estimate $\pm$ SE = -63.40 ± 16.88, Wald $\chi_1^2 = 14.10$, $P < 0.001$, $r = 0.751$, CI lower = 0.491, CI upper = 0.871).

Assuming a gradual mode of evolution in the parts of the phylogenetic tree without information on branch length in general yielded qualitatively identical results to the ones shown above. However, after sequential

Table 2 Relationship between allometry of ornamental feathers and migration distance, mating system and relative size of ornaments in bird species with ornamental tail feathers.

Sex	n	Variable	Estimate	SE	Wald statistic	d.f.	P	r	CI lower	CI upper
Males	31	Migration distance	−0.10	(0.05)	3.67	1	0.056	0.344	−0.011	0.607
		Mating system	−0.12	(0.05)	6.40	1	0.011	0.454	0.116	0.681
		Relative size of ornament	−0.23	(0.18)	1.72	1	0.19	0.236	−0.124	0.530
Females	25	Migration distance	0.00	(0.04)	0.00	1	0.99	0.003	−0.377	0.383
		Mating system	−0.21	(0.06)	13.42	1	< 0.001	0.733	0.461	0.861
		Relative size of ornament	−0.38	(0.18)	4.52	1	0.033	0.425	0.035	0.683

Sample size is number of independent contrasts.

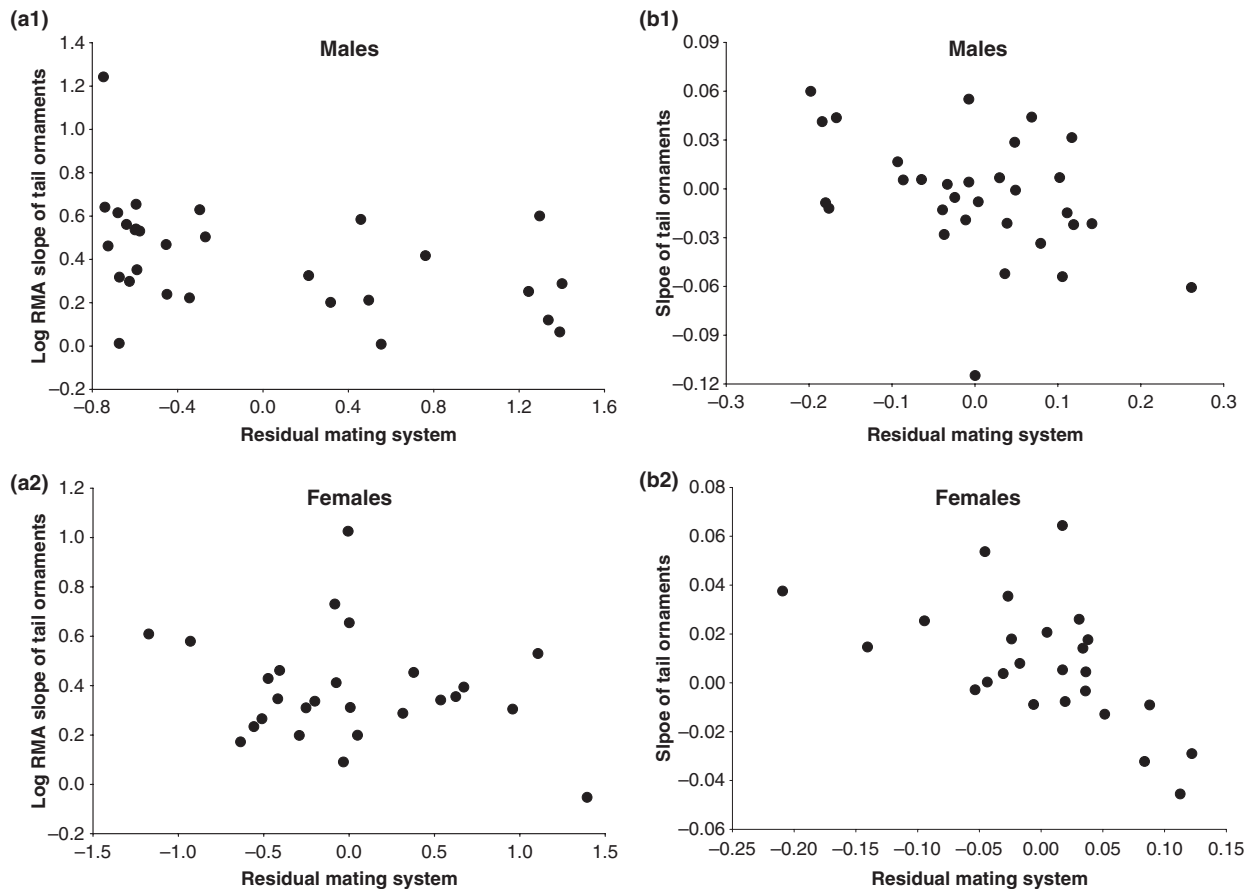**Fig. 3** Log_{10}-transformed reduced major axis slope of tail ornaments in relation to residual mating system (residuals from regressing mating system on migration distance and relative size of tail ornaments) in male and female birds, with each data point representing (a) a species or (b) an independent contrast.

Bonferroni correction ($k = 6$), the RMA slope of male ornamental feathers was negatively related to migration distance when including all species in the analysis ($n = 66$, estimate ± SE = $-0.16 ± 0.07$, Wald $\chi_1^2 = 5.89$, $P = 0.015$, $r = 0.299$, CI lower = 0.061, CI upper = 0.504), and marginally nonsignificantly related to migration distance when only including species with ornamental tail feathers ($n = 31$, estimate ± SE = $-0.13 ± 0.06$, Wald $\chi_1^2 = 5.67$, $P = 0.017$, $r = 0.428$, CI lower = 0.084, CI upper = 0.664). The latter relationship became statistically significant after sequential Bonferroni correction ($k = 6$), when sedentary species were excluded from the analysis ($n = 9$, estimate ± SE = $-0.10 ± 0.04$, Wald $\chi_1^2 = 7.21$, $P = 0.0073$, $r = 0.895$, CI lower = 0.530, CI upper = 0.962). Therefore, the relationship between the RMA slope of male ornaments and migration distance depended on the phylogenetic assumptions, unless we consider only tail feather ornaments of migratory species, in which case the relationship was negative and statistically significant for the two phylogenetic assumptions.

Discussion

One of the main findings of this study was that male ornamental feathers in birds generally showed positive allometry, i.e. ornaments were disproportionately large in large individuals. This result is in agreement with a number of previous studies showing positive allometry for secondary sexual characters, both ornaments (e.g. Echelle *et al.*, 1978) and weapons (e.g. Kawano, 1997). Moreover, the allometric slope of male ornamental feathers was significantly greater (more positive) than that of nonornamental (wing, tail) feathers. However, our study also found positive allometry for some non-sexual characters. First, positive allometry was found in female traits homologous to male ornaments, although these traits probably do not have a signalling function. A genetic correlation between the sexes can explain the expression of exaggeratedly long feathers in females even if they are not the direct target of selection (Lande, 1980). Therefore, an elevated allometry of female homologous characters might be expected as the result of a genetic

correlation between the sexes. However, our data suggest that the allometry of female feathers homologous to male ornaments is as large as the allometry of male ornaments or even larger (see Table 1 and the Appendix), and intersexual genetic correlation alone cannot explain this pattern. Second, the allometry of nonornamental tails was positive, thus clearly contradicting the idea that nonsexual characters should only show isometry or negative allometry. We can speculate that the role of tail feathers in flight is responsible for this pattern, because previous studies have shown positive allometries for locomotory traits due to biomechanical factors (Tseng & Rowe, 1999). However, wing feathers, although also being essential for flight, did not show positive allometry but instead isometry (or negative allometry if species with very large slopes were excluded from the analysis). Consequently, this study does not support theoretical models predicting positive allometry for secondary sexual characters and isometry or negative allometry for non-sexual characters (Kodric-Brown *et al.*, 2006). Our results are however consistent with theoretical models that predict any kind of allometric pattern, including positive allometry, for both sexual and nonsexual characters (Bondurianksy & Day, 2003).

Another consequence of our results is that the peculiar positive allometry of nonornamental tail feathers may have facilitated the disproportionately large number of cases of evolution of exaggerated tails in birds. We found that both nonornamental and ornamental tail feathers showed positive allometry, and we suggest that ornamental tail feathers might evolve as a consequence of positive allometry for nonornamental tail feathers. If nonornamental tail feathers generally show positive allometry, any change in ecological conditions that reduced the cost of exaggerated traits would facilitate rapid increase in size. In contrast, that would not be the case for traits showing isometric or negative allometric relationships. This prediction is open to empirical test.

The results of this study are completely different from the ones obtained by Cuervo & Møller (2001). Our previous study found that the allometries of both ornamental and nonornamental feather traits were negative, i.e. allometry coefficients were smaller than 1. In contrast, the present study shows that ornamental and also some nonornamental traits (e.g. tail feathers) show positive allometry (allometry coefficients > 1). The only methodological difference between the two studies was the way of estimating allometry, OLS vs. RMA slopes, and, consequently, the type of slope seems to be the only factor responsible for the difference in results. As explained in the Introduction, OLS slopes tend to underestimate allometry and, thus, RMA slopes represent better estimates of allometry, at least in our case. It should be noted, however, that overemphasizing the importance of comparing absolute slopes with the usual reference value of 1.00 can be misleading for a number of reasons (Eberhard *et al.*, 2009). Comparisons of orna-

mental and nonornamental traits within species might be more appropriate (Eberhard *et al.*, 2009), but we also followed this approach and found that the results depended on the type of slope used to estimate allometry. While OLS slopes suggested that the allometries of ornamental and nonornamental feathers did not differ significantly (Cuervo & Møller, 2001), RMA slopes show that allometry is greater (more positive) in ornamental than in nonornamental feathers (this study). Therefore, choosing the correct estimate of allometry is crucial in allometry studies.

Bonduriansky (2007) argued that the preponderance of positive allometries for secondary sexual characters in the literature was caused by biased sampling, because allometric patterns have been studied mainly in species with extremely exaggerated ornaments or weapons. The bird species included in our study show extreme feather length exaggeration in some cases (e.g. the tail coverts of *Pharomachrus mocinno* or *Pavo cristatus*), but very small ornaments in others (e.g. the moustaches of *Malurus splendens* or *Panurus biarmicus*; see relative size of male ornaments in the Appendix). Therefore, our sample is not biased in this respect (but see below). Moreover, the variety of ornament sizes allowed us to test the prediction, implicit in Bonduriansky's (2007) argument, that allometric slopes would be positively related to the relative size of ornaments. However, this prediction did not come true for the feather ornaments studied here. In fact, we found the opposite trend in a particular case, because there was a negative, marginally nonsignificant relationship between the allometric slope of tail feather ornaments and the relative size of these characters in females. This means that the increase in tail length with body size tended to be less pronounced for long than for short tails. Ornamental tail feathers in females showed negative allometry in some species ($n = 6$) but positive allometry in others ($n = 15$) (see Fig. 2 and the Appendix). As a result, tail ornaments tended to be more costly for small than for large females in species with long tail ornaments, but more costly for large than for small females in species with short tail ornaments. If allometry was positive in all species, tail ornaments would always be more costly for large than for small females, and the negative trend shown above would mean that tail ornaments were disproportionately more costly for large females in species with short tail ornaments. In any case, only female traits homologous to male ornaments, but not male ornaments themselves showed this trend.

We would like to emphasize that our study is unique by constituting the only exhaustive sample of species with exaggerated secondary sexual characters, thus excluding the possibility that the general patterns of allometry that we detected were biased due to sampling. However, only feather traits at least 5% different in mean length between the sexes were considered to qualify as ornaments. Consequently, feathers with sexual size dimorphism smaller than 5%, including sexually size

monomorphic traits, have been excluded from the study. This selection criterion might have potentially introduced a bias if sexual ornaments with less and more than 5% sexual size dimorphism differed in pattern of allometry. We know already that sexual size dimorphism is positively related to the size of male feather ornaments (Cuervo & Møller, 2000), but we have shown here that relative size and the RMA slope of male ornaments are not significantly related. Therefore, there is no indication that the degree of sexual size dimorphism could have affected the allometric pattern of ornaments. However, the possibility of bias due to our definition of ornamental feather cannot be completely ruled out.

The two groups of ornaments that we considered here, head/neck and tail feathers, do not only differ in size, but also in function. Head/neck feathers are ornaments with an exclusive sexual function, termed 'dedicated' secondary sexual traits by Bonduriansky (2007). In contrast, tail feather ornaments, despite having been modified by sexual selection, still play an important role in flight (the ancestral function), and, thus, these feathers have both a sexual and a nonsexual function. According to Bonduriansky (2007), dedicated secondary sexual traits should tend to show positive allometry, because their costs decrease as body size increases, while secondary sexual traits with viability-related functions tend to show negative allometry or isometry, because their costs are relatively body size independent. Clearly, that was not the case for tail feather ornaments, because they also showed positive allometry in this study. We found no significant difference in allometric slope between head/neck and tail feather ornaments.

We suggested that migration distance between breeding and wintering grounds would affect the allometry of feather ornaments. A negative relationship between the two variables was expected because flight (and, thus, migration) is a very costly activity (Norberg, 1990), and any increase in ornament length would be more costly for long- than for short-distance migrants. Indeed, in the case of tail feather ornaments in males of migratory species, a negative relationship between allometric slope and migration distance was found. However, when all species were included in the analyses, the relationship was significant only when we assumed a gradual mode of evolution in the parts of the phylogenetic tree without information on branch length. In the case of homologous characters in females, the relationship between allometric slope and migration distance was not statistically significant. Although these results should be interpreted with caution, mainly because different phylogenetic assumptions or different subsets of species provided different results, they suggest a trend for more negative allometry of male feather ornaments with greater migration distance. This trend was in the expected direction, i.e. an increase in the costs of a secondary sexual trait with a decrease in the allometric slope of that trait.

Both the mode (directional or stabilizing) and the strength of selection have been hypothesized as basic factors determining the allometric relationship between trait size and body size (Green, 2000; Kodric-Brown et al., 2006). Feather ornaments are subject to directional sexual selection, and the strength of selection is determined by variation in mating success. According to the degree of variation in male mating success, avian species can be categorized as having three mating systems: monogamy, polygyny and lekking. Social monogamy does not imply genetic monogamy, because extra-pair paternity is common in many bird species (Birkhead & Møller, 1992). However, variation in male mating success is assumed in general to be smaller in monogamous than in polygynous species, and smaller in polygynous than in lekking species. Although we expected the allometric slope of ornaments to be greater (more positive) when mating success was more skewed, our expectation was not met. In contrast, the opposite result was found in the group of birds with ornamental tail feathers. The allometric slope of male and female tail ornaments was negatively related to variation in male mating success, i.e. to the strength of sexual selection. In other words, tail ornaments showed more positive allometry in monogamous than in polygynous or lekking species. The relationship between the allometric slope of tail ornaments and mating system was tested while simultaneously controlling for the possible effect of the relative size of the ornament, and, therefore, it was statistically independent of ornament size. These results suggest that investment in tail feather ornaments by small and large males is more similar in polygynous and lekking species than in monogamous ones. We do not have an explanation for this finding, but we speculate that small males in species with skewed male mating success should invest relatively more in ornamentation because that is the only way for them to gain a mating opportunity. While small ornamented males may have even a high probability of mating in monogamous species, they have practically no chance in lekking species with a very skewed distribution of male mating success.

In summary, we found that sexually size dimorphic feather ornaments in birds show positive static allometry, but some nonornamental feathers (female traits homologous to male ornaments and nonornamental tail feathers) also show positive allometry. An increase in the strength of sexual selection seems to be associated with a reduced allometric slope of ornaments in some cases, particularly for tail feather ornaments that are relatively large characters with viability-related functions. The cost of ornamentation might also play a role in moulding the patterns of allometry, with an increase in the cost associated with a decrease in allometric slope, although our results are not conclusive in this respect. This study does not support theoretical models predicting positive allometry for secondary sexual characters, but isometry or negative allometry for nonsexual characters (Kodric-Brown et al., 2006). However, it is consistent with other models that do not

predict any particular relationship between the kind of trait (sexual vs. nonsexual) and the allometric pattern (Bonduriansky & Day, 2003).

Acknowledgments

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Appendix

Information on type of ornamental feather, reduced major axis slopes, relative size of ornament, migration distance (degrees latitude) and mating system for the 67 species included in this study. Ornamental feathers were grouped in three categories: tail rectrices (T), head and neck feathers (H) and others (O). Mating systems were categorized as social monogamy (0), polygyny (1) and lekking (2). For definition and calculation of these variables, see Materials and methods.

Species	Type of ornamental feather	Slope of male wing	Slope of male tail	Slope of male ornament	Slope of female wing	Slope of female tail	Slope of female ornament	Relative size of male ornament	Relative size of female ornament	Migration distance	Mating system
Aglaiocercus kingi	T	0.86	–	3.84	0.88	–	2.27	1.32	0.82	0	1
Amblyornis subalaris	H	0.49	0.71	1.78	–	–	–	0.04	–	0	2
Anairetes reguloides	H	0.98	3.61	3.93	0.45	0.45	2.18	−0.05	−0.09	0	0
Anas falcata	O	0.55	2.10	1.52	0.52	1.62	3.49	0.68	0.44	20.00	0
Anas platyrhynchos	T	1.28	1.01	3.08	–	–	–	0.17	–	8.13	0
Anthochaera carunculata	T	1.50	–	2.89	1.10	–	1.49	0.67	0.64	0	0
Aplonis metallica	T	0.40	–	1.67	0.88	–	1.71	0.65	0.62	5.50	0
Aythya fuligula	H	0.98	1.96	5.88	1.42	2.39	25.21	0.26	−0.14	17.08	0
Cardinalis cardinalis	H	1.04	1.69	2.20	0.99	1.34	2.52	0.09	0.07	0	0
Chiroxiphia linearis	T	0.26	–	1.32	0.86	1.57	3.39	0.89	0.47	0	2
Clangula hyemalis	T	0.91	–	3.40	–	–	–	0.77	–	15.78	0
Copsychus malabaricus	T	1.03	–	4.13	1.31	–	1.85	0.82	0.73	0	0
Coracias abyssinicus	T	0.39	0.72	1.73	0.66	0.89	1.23	1.02	1.01	1.00	0
Dicrurus paradisaeus	T	0.94	–	3.47	0.65	–	1.58	1.13	1.09	0	0
Dinopium javanense	H	1.52	1.81	1.68	0.81	1.07	3.22	0.01	−0.01	0	0
Diphyllodes magnificus	H	1.67	3.52	5.74	–	–	–	0.11	–	0	2
Dryoscopus sabini	O	0.72	0.59	0.90	1.57	2.67	3.80	0.14	0.12	0	0
Eremophila alpestris	H	0.53	1.23	1.68	0.73	1.01	2.17	−0.37	−0.44	11.47	0
Erythrura prasina	T	0.71	–	4.38	0.68	–	3.80	0.61	0.45	0	0
Euplectes jacksoni	T	0.79	–	2.27	–	–	–	0.84	–	0	2
Gallus gallus	H	0.93	–	2.40	0.86	1.24	2.40	0.18	−0.04	0	1
Hirundo rustica	T	1.06	–	2.11	0.60	–	2.05	0.99	0.91	42.34	0
Hirundo semirufa	T	0.87	–	3.19	0.72	–	2.17	0.91	0.86	5.50	0
Hydrophasianus chirurgus	T	1.17	–	2.61	0.92	–	2.20	0.71	0.67	9.00	1
Hydropsalis brasiliana	T	1.16	–	3.39	0.75	–	2.04	1.19	0.90	0	0
Lophorina superba	O	0.73	0.70	1.87	–	–	–	0.57	–	0	2
Lophortyx californica	H	0.61	0.82	1.72	1.01	2.98	5.39	0.04	−0.16	0	0
Macrodipteryx longipennis	O	0.78	–	3.14	–	–	–	1.36	–	0.50	1
Malurus splendens	H	0.63	1.14	2.44	–	–	–	−0.42	–	0	0
Melophus lathami	H	0.63	1.73	2.08	1.03	1.74	3.09	0.07	−0.10	0	0
Menura novaehollandiae	T	0.75	–	3.98	1.02	–	0.89	0.74	0.66	0	2
Nectarinia johnstoni	T	1.22	–	3.64	–	–	–	0.97	–	0	0
Orthotomus sutorius	T	3.60	–	17.47	1.58	–	4.07	0.59	0.29	0	0
Otis tarda	H	0.56	0.61	2.18	0.68	0.79	6.72	−0.08	−0.70	0.10	2
Oxypogon guerinii	H	0.66	1.07	3.24	–	–	–	0.43	–	0	1

Appendix

(*Continued*).

Species	Type of ornamental feather	Slope of male wing	Slope of male tail	Slope of male ornament	Slope of female wing	Slope of female tail	Slope of female ornament	Relative size of male ornament	Relative size of female ornament	Migration distance	Mating system
Panurus biarmicus	H	0.76	1.63	2.02	0.54	1.38	2.54	−0.23	−0.33	0	0
Paradisaea rubra	T	0.74	–	1.16	–	–	–	1.08	–	0	2
Parotia lawesii	O	0.67	–	1.14	–	–	–	−0.30	–	0	2
Pavo cristatus	O	0.36	1.08	1.53	–	–	–	1.05	–	0	2
Phainopepla nitens	H	0.67	0.79	1.13	0.96	1.19	1.59	0.15	0.06	0.50	0
Pharomachrus mocinno	O	0.32	–	1.57	1.57	–	3.74	1.55	0.93	0	0
Phasianus colchicus	T	0.56	–	1.59	0.90	–	2.84	0.81	0.65	0	1
Philomachus pugnax	H	1.01	1.67	4.96	–	–	–	−0.11	–	52.21	2
Pipra cornuta	H	1.04	1.48	3.42	–	–	–	−0.07	–	0	2
Pithys albifrons	H	0.55	1.91	3.69	1.16	2.33	4.91	−0.03	−0.10	0	0
Podiceps cristatus	H	0.55	–	2.47	0.69	–	2.88	−0.20	−0.23	4.41	0
Prosthemadera novaeseelandiae	H	1.54	1.89	3.09	0.72	0.78	1.54	−0.06	−0.07	0	0
Psalidoprogne obscura	T	0.40	–	1.99	0.34	–	1.58	1.02	0.87	0	0
Psittacula longicauda	T	0.83	–	2.25	1.05	–	5.38	1.14	1.01	0	0
Pteridophora alberti	H	1.24	1.43	4.26	–	–	–	1.14	–	0	2
Ptilogonys caudatus	T	0.61	–	2.08	1.18	–	2.89	0.85	0.79	0	0
Ptiloris magnificus	O	0.59	1.11	2.79	0.80	0.73	1.96	0.64	0.29	0	2
Quiscalus mexicanus	T	0.39	–	1.02	1.14	–	1.94	0.60	0.56	3.00	1
Rollulus rouloul	H	1.85	4.51	7.83	–	–	–	−0.06	–	0	0
Rupicola peruviana	H	0.43	0.60	1.65	0.54	0.32	2.35	−0.11	−0.27	0	2
Scotornis climacurus	T	0.87	–	3.44	0.89	–	2.58	1.11	1.01	0	0
Semioptera wallacei	O	0.72	2.46	2.18	–	–	–	0.57	–	0	2
Sturnus unicolor	H	0.48	1.68	4.95	0.59	1.16	4.17	0.04	−0.11	0	1
Tanysiptera galatea	T	1.70	–	4.51	2.67	–	10.60	1.13	1.06	0	0
Terpsiphone viridis	T	0.79	–	2.94	0.71	–	2.68	1.21	0.73	0.50	0
Tetrao tetrix	T	0.48	–	1.79	1.06	–	2.02	0.56	0.38	0	2
Topaza pella	O	1.58	–	4.09	–	–	–	0.34	–	0	2
Treron apicauda	T	0.75	–	1.03	0.62	–	2.22	0.85	0.79	0	0
Trochilus polytmus	T	0.64	–	1.63	0.70	–	2.48	1.44	0.85	0	1
Tyrannus savana	T	1.16	–	4.26	0.97	–	4.51	1.13	1.01	3.00	0
Vanellus vanellus	H	0.91	2.06	4.59	1.08	1.36	8.55	0.19	0.02	12.08	0
Vidua macroura	T	0.86	–	1.94	–	–	–	1.11	–	0	2