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SPECIATION AND FEATHER ORNAMENTATION IN BIRDS

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Abstract.—The hypothesis that sexual selection promotes speciation has rarely been tested. We identified 70 evolutionarily independent events of feather ornaments in birds. For each focal species we noted the number of ornamented and nonornamented species belonging to its genus and its number of subspecies, as well as its mating system and the extent of its geographic range. For purposes of comparison, we randomly chose a second, nonornamented species for which we obtained information on the number of subspecies, and in cases in which the nonornamented species was in the same genus, we chose a third, nonornamented species in a related genus and obtained the same information. We then noted the number of species in each genus and the difference in numbers of species, or species richness, between paired genera. For the genera of the focal ornamented species, we regressed number of ornamented species on number of nonornamented species and found a positive relationship. As number of species per genus rose, number of ornamented species per genus rose more rapidly, indicating that more speciose genera have a higher proportion of ornamented species than less speciose genera. We then took the deviations from this regression, the residual number of species, and regressed them on the differences in species richness between the paired genera. This relationship was positive indicating that ornamented genera with more than the expected number of ornamented species were more speciose with respect to their paired genera than were genera with fewer than the expected number of ornamented species. Finally, we compared the deviations from this regression, the residual number of ornamented species, with species' mating system and found a greater residual number of ornamented species among species whose mating system is associated with greater skew in male mating success and thus more intense sexual selection. Ornamented species had more subspecies than nonornamented species, even when controlling for geographic range, suggesting an association between subspeciation and ornaments.

Key words.—Feather ornaments, Fisherian mechanism, indicator models, runaway process, sexual selection, viability models.

Speciation has been assumed to result from sexual selection since Darwin (1871; M. Andersson 1994). The mechanism leading to such diversification has been presumed to be female mate preferences that may enhance the rate of reproductive divergence between populations and thereby increase the diversity of a clade (Darwin 1871; Fisher 1930; Carson 1978, 1986; Kaneshiro 1980, 1989; Lande 1981, 1982; West-Eberhard 1983; Dominey 1984; Schluter and Price 1993). Because females with the strongest preferences tend to mate with males with the most extreme expression of the male trait (assortative mating), female mate preference and male trait may become correlated within populations (Fisher 1930). Trait expression becomes more extreme in a runaway fashion until sexual selection is balanced by oppositely directed natural selection pressures. Rapid divergence between populations in the expression of the female preference and the male secondary sexual character by the Fisherian process may lead to speciation (Lande 1981, 1982).

Sexual selection based on viability-indicator models may also give rise to divergence and speciation (Schluter and Price 1993). The proposed mechanism is that environmental differences can drive evolutionary divergence between populations in both the male trait and the female preference, and even small differences between habitats in the contrast between male coloration and the color of the habitat can trigger dramatic changes in the female preference (Schluter and Price 1993). The two models of speciation by sexual selection differ in that the Fisherian mechanism will be more important in cases of extreme skew in male mating success. If mating success is extremely skewed, this will invariably lead to depletion of genetic variation in fitness (Charlesworth 1987; Burt 1995), which might reduce the likelihood of any effects of sexual selection due to good genes (the viability-indicator mechanism). A recent review of laboratory studies of mechanisms of speciation concluded that sexual selection was an important component of speciation (Rice and Hostert 1994).

There are few rigorous empirical tests of the hypothesis that sexual selection promotes speciation. Support has instead come from classical examples of clades that are both speciose and possess elaborate courtship displays, such as Hawaiian *Drosophila*, species swarms of cichlids in Africa, birds of paradise, and amphibians (Carson 1978; West-Eberhard 1983; Dominey 1984; Ryan 1986). Obviously, we cannot use such examples as rigorous tests, simply because there are too few to allow formal statistical analyses, and many factors other than sexual selection may be correlated with an increase in species richness in each of these cases.

Two published comparative studies have addressed the association between speciation and sexual selection. First, a comparative study relating sexual dichromatism in birds to species richness revealed larger numbers of species in taxa containing higher proportions of sexually dichromatic species (Barraclough et al. 1995). Second, a study comparing species richness in promiscuous avian taxa to sister taxa with mating systems with less skew in male mating success showed a tendency at the borderline of statistical significance toward larger numbers of species in the promiscuous taxa (Mitra et al. 1996).

Here we use feather ornaments in birds to test whether speciation is related to sexual selection. We operationally

defined feather ornaments as any feather trait that differed in length between males and females by at least 5% or that was expressed only in males. Several studies of mate choice have demonstrated that females prefer males with longer feathers, thus demonstrating that feather ornamentation can be maintained as a consequence of female mate preferences (e.g., M. Andersson 1982; Møller 1988, 1994; Barnard 1990; Petrie et al. 1991; S. Andersson 1992; Evans and Hatchwell 1992). A meta-analysis of the literature on sexual selection in relation to secondary sexual characters such as feather ornaments revealed an intermediate average correlation between male ornamentation and female choice when adjusted for sample size (Pearson's $r = 0.43$, an effect of an intermediate magnitude; M.-C. Gontard-Danek and A. P. Møller, unpubl. data). Considerable amounts of the residual variation were explained by whether a study consisted of observations or experiments and by the species' social mating system. Thus, while we know that female preferences can be associated with male ornamentation, we are less clear on whether this might lead to speciation.

To address this question we identified from field guides and visits to museum collections 82 species, which upon close scrutiny were reduced to 70 independent evolutionary events of feather ornamentation in birds based on the phylogeny of Sibley and Ahlquist (1990) as well as more rigorous phylogenies for some groups (see Materials and Methods). This database was used to test the following predictions. (1) The number of species in a genus that contains at least one ornamented species will be larger than in a sister genus without ornamentation. (2) If ornamentation is responsible for speciation, then the difference in number of species between ornamented and nonornamented sister genera should be positively correlated with the excess number of species in the ornamented genera, where excess is defined as the residuals in a regression of the number of ornamented species on the number of nonornamented species. (3) If sexual selection leads to divergence between populations, then the number of subspecies per species should be larger in ornamented than in nonornamented species in the ornamented genera. (4) If the Fisherian mechanism is responsible for speciation, we should expect speciation to be particularly evident in avian taxa with a more extreme skew in male mating success. Hence species richness should increase along an axis of increasing skew, from socially monogamous species to polygynous species and particularly to lekking species.

Materials and Methods

Independent Evolution of Feather Ornamentation

We defined feather ornaments as any feather trait that differed in length between males and females by at least 5% or that was expressed only in males. For references consulted see Appendix 1. For all families and orders that have been treated in monographs, we had complete knowledge of the number of potentially ornamented species. For the remaining families, we used information in field guides combined with extensive use of major European museum collections to check for cases of ornamentation. For all species with any indication of feather traits being exaggerated, we checked whether the species conformed to our definition of orna-

mentation and whether it represented an independent evolutionary event, using the phylogenetic information described below. Examples of feather ornaments included long tails but also exaggerated crests, wing plumes, tail coverts, and head feathers. This exhaustive list of species with feather ornaments was used as a baseline.

We determined the number of evolutionarily independent events of feather ornamentation that have arisen independently according to Sibley and Ahlquist's (1990) phylogeny of birds. Sibley and Ahlquist have been criticized for their methods (e.g., Krajewski 1991; O'Hara 1991; Raikow 1991), and we therefore assessed the reliability of this source by using independent phylogenetic information for the families Anatidae, Hirundinidae, Phasianidae, Ptilorhynchidae, and Trochilidae (phylogenies in Livezey 1986; Randi et al. 1991; Kusmierski et al. 1993; Winkler and Sheldon 1993; Bleiweiss et al. 1994). The supplemental phylogenies identified three cases of independent evolutionary events that were not identified using the phylogeny by Sibley and Ahlquist, and no cases identified by Sibley and Ahlquist were unsupported by the alternative phylogenies. Hence, by mainly relying on Sibley and Ahlquist (1990) we have used a conservative estimate of the number of evolutionary events.

Using the phylogenetic information we identified a total of 82 potential cases of feather ornamentation representing 13 orders, 41 families, and 68 genera. Some species were borderline cases with apparently little sexual size dimorphism, but we investigated these by measuring 10 males and 10 females in major European museum collections. Twelve cases were eliminated because they were sexually size monomorphic based on these measurements (the size of the character in males differing from that of females by less than 5%). The degree of sexual size dimorphism (the difference in morphological characters between males and females) among the species included in the present study was on average 68.4% (SE = 13.4, $n = 49$ species). The ornament was present only in males in the remaining species. If more than one trait had become exaggerated in a family, we considered this to represent a number of independent evolutionary events equaling the number of exaggerated traits. If, for example, a long tail was found in some species of a family and long crest feathers were found in other species, these occurrences were tallied as two independent evolutionary events of feather ornamentation. We excluded cases of extravagant feather characters in both sexes when there was no sexual size dimorphism, even though mutual sexual selection may account for such exaggerated monomorphism (Jones and Hunter 1994).

Species Richness

For each of the ornamented species we randomly chose a second, nonornamented species for estimates of the number of subspecies (see below). If this nonornamented species was in the same genus as the ornamented species, we randomly chose a third, nonornamented species in a related genus for analysis of species richness.

The number of ornamented and nonornamented species in each pair of ornamented and nonornamented sister genera was obtained from information in Howard and Moore (1991).

If we were uncertain whether a particular species within a genus was ornamented, as defined above, we classified it as nonornamented. Thus the number of ornamented species per genus represents a minimum estimate. The data are reported in Appendix 2.

Number of Subspecies and Breeding Range

To estimate intraspecific divergence, we compared the number of subspecies in the ornamented species and in a randomly chosen nonornamented species within each clade, based on information in Howard and Moore (1991). The number of subspecies described may depend on the extent to which different species have been the subject of detailed studies. However, birds have been the target of extensive taxonomic studies dating back several centuries, and birds are by far the best known class of animals. We see no a priori reason why differences in the extent of study of different species should lead to a consistent bias toward the description of more subsepcies in species that are ornamented. The data on the number of subspecies are reported in Appendix 2.

To control for the potential effects of size of the breeding range on the number of subspecies, we estimated the breeding ranges of the ornamented and nonornamented species from distribution maps in the source references (Appendix 1) as the difference in latitudinal degrees between the northern and the southern limits of the species' breeding distribution.

Mating System

We obtained information on the mating system of the species of ornamented and nonornamented species directly from the source references (Appendix 1). Species were classified as follows: (1) monogamous if males mated with a single female or in fewer than 5% of cases with more than one female; (2) polygynous if males mated with more than one female more frequently than in 5% of reported cases; and (3) lekking if males aggregated at communal display grounds where females arrived for making their mate choice. The information is given in Appendix 2.

Statistical Analyses

We compared the number of species in randomly chosen species with ornaments with the number of species in a randomly chosen sister genus. Because the number of species in such paired genera with and without feather ornaments was not normally distributed, we used a nonparametric Wilcoxon test for the comparison of species richness of the pairs of genera (Siegel and Castellan 1988).

If species richness within genera is directly related to the presence of feather ornaments, we would predict that the most speciose genera would be those with the highest proportion of ornamented species. For the set of genera containing the 70 ornamented species, we first regressed the number of ornamented species on the number of nonornamented species. The residuals from this regression provided an estimate of the relative abundance of ornamented species, while controlling for overall species richness. That is, positive values represented genera that were disproportionately rich in ornamented species, while negative values represented genera

that were poor in ornamented species. We treated the residuals as a variable called residual number of species. To test the null hypothesis of no association between the residual number of species in ornamented genera and species richness within ornamented genera compared to their nonornamented sister genera, we regressed the residual number of species on the difference in species richness between the genera containing the ornamented species and their nonornamented reference genera.

We tested for intraspecific divergence (the number of subspecies) in relation to feather ornamentation by regressing the $\log_{10}$-transformed number of subspecies on the $\log_{10}$-transformed breeding range of a species. The residuals from this regression provided an unbiased estimate of number of subspecies corrected for geographical range. A paired t-test was used to determine whether the relative number of subspecies corrected for breeding range was larger in ornamented than in the nonornamented paired genera.

To test for a relationship between mating system and species richness we returned to the regression of residual number of species on difference in species richness and computed the residuals from this regression. These were treated as a variable called the residual number of ornamented species. Positive residuals imply a relatively large number of species for a given level of difference in species richness, whereas negative residuals imply a relatively small number of species. We used these residuals as our measure of speciation mediated by sexual selection and related them to the mating system (scored as 0 [monogamous], 1 [polygynous], or 2 [lekking]). Since the mating system variable was not normally distributed, we used Kendall rank order correlation analysis to test for an increase in species with increasing presumed skew in mating success (Siegel and Castellan 1988).

RESULTS

Speciation and Sexual Selection

Ornamented taxa were more speciose compared to their nonornamented sister taxa (mean [SE] number of species in ornamented genera = 8.31 [1.43], in nonornamented genera = 4.46 [1.12], difference = 3.85 [1.80]; Wilcoxon matched-pairs signed-ranks test, $z = -3.57$, $n = 68$, $P < 0.001$). On average, there were 1.86 times as many species in the ornamented as the non-ornamented taxa.

Within ornamented genera, the number of ornamented species increased with the number of nonornamented species (Fig. 1; linear regression: slope (SE) = 0.097 (0.047), $F = 4.22$, df = 1,67, $r^2 = 0.060$, $P = 0.044$). The fit was not improved by using log-transformed variables. The relationship between the residual number of species (defined as the residuals from the linear regression above) and the difference in species richness between ornamented genera and their non-ornamented related genera was statistically significant and positive (Fig. 2; slope (SE) = 0.084 (0.031), $F = 7.43$, df = 1,67, $r^2 = 0.101$, $P = 0.0082$). The positive association implies that the increase in the number of species is directly related to the disproportionate number of ornamented species in species-rich genera (Fig. 2).
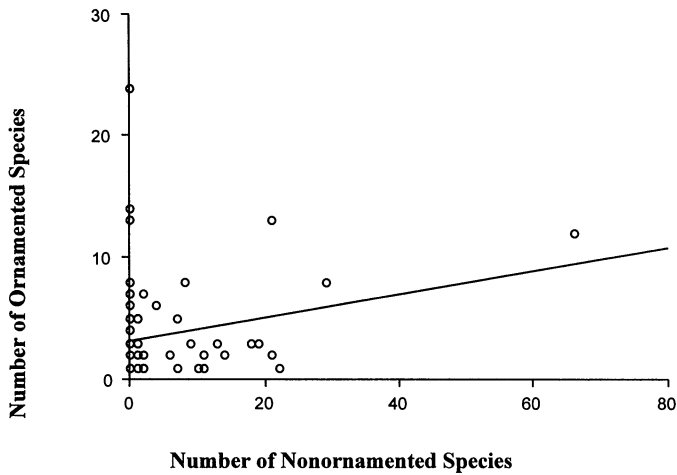
FIG. 1. Linear regression of the number of ornamented bird species on the number of nonornamented species for 70 avian genera containing at least one ornamented species. The relationship is positive, and the slope of the regression line is 0.097 (SE = 0.047), F = 4.22, df = 1,67, r^2 = 0.060, P = 0.044.

Number of Subspecies and Ornamentation

The relationship between the log-transformed number of subspecies and the log-transformed breeding range was highly significant: F = 25.79, df = 1,139, r^2 = 0.157, P < 0.001, slope (SE) = 0.387 (0.076). The residuals from this regression line had on average larger values for ornamented than for nonornamented species (ornamented species [mean (SE)]: 0.048 [0.045], n = 70; nonornamented species: −0.048 [0.036], n = 70; paired t-test, t = 1.99, df = 69, P = 0.05).

Speciation and Mating System

The correlation between the residual number of ornamented species and mating system was positive and statistically significant (Fig. 3; Kendall rank order correlation: τ = 0.19, n = 67, z = 2.32, P = 0.020).

Genera with ornamented polygynous and lekking species had a significantly larger residual number of ornamented species than genera with ornamented monogamous species (Mann-Whitney U-test, monogamous [mean (SE)]: −0.483 [0.541], n = 38, lekking: 0.520 [0.763], n = 29, z = −2.12, P = 0.034). Polygynous and lekking species did not differ significantly in residual number of ornamented species (Mann-Whitney U-test, z = −0.047, P = 0.96).

DISCUSSION

We tested whether species richness was related to sexual selection by comparing the number of species in ornamented and nonornamented genera. Species richness was on average 1.86 times greater in the ornamented genera (Table 1). Similar differences in species richness have previously been associated with sexual dichromatism (Barraclough et al. 1995) and lekking (Mitra et al. 1996) in birds. Genera with more species have disproportionately more ornamented species. Variation in species number not explained by this general trend was positively related to the degree to which an ornamented genus differed in species richness from a randomly
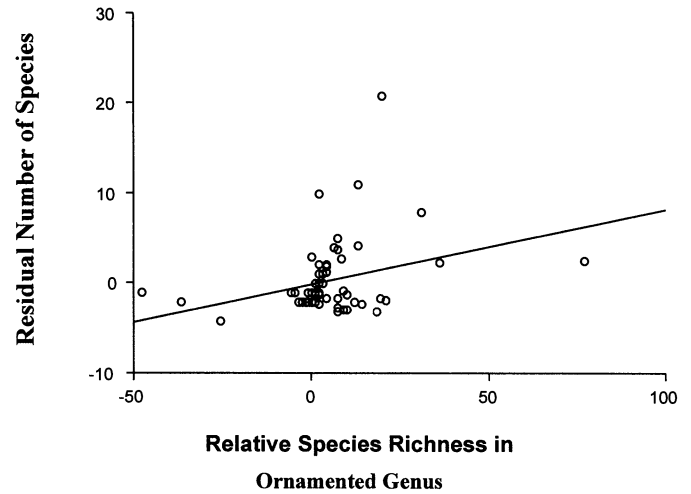

FIG. 2. Residual number of bird species (residuals from a regression of the number of ornamented species per genus on the number of nonornamented species per genus; see Fig. 1) in relation to relative species richness in ornamented genera (difference in the number of species in ornamented genera as compared to their matched nonornamented sister genera). The relationship is positive, and the slope of the regression line is 0.084 (SE = 0.031), F = 7.43, df = 1,67, r^2 = 0.101, P = 0.0082.

chosen reference genus. This implies that ornamented genera have more species because they contain higher proportions of ornamented species. This result is consistent with a direct role of sexual selection in the process of diversification. Although the regression was highly statistically significant, only 10.1% of the variance in residual number of species was explained by the regression on the intergeneric difference in species richness. Hence, a number of additional factors are likely to determine the level of speciation. We have investigated only feather ornaments in the present study, but birds have a number of other sexual displays, such as bright coloration, song, and courtship. Variation in these types of dis-
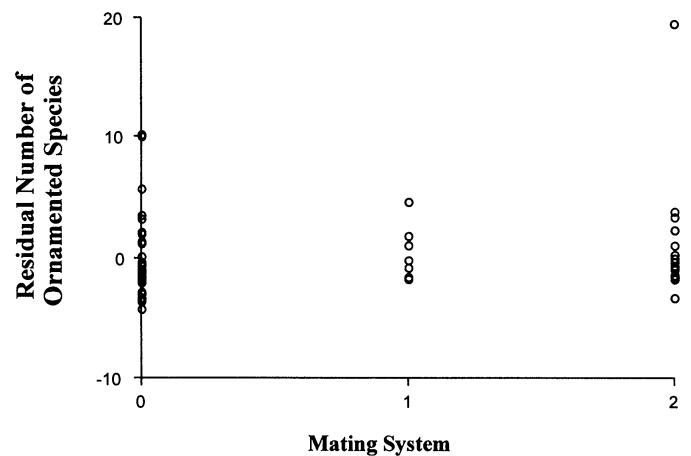

FIG. 3. Residual number of ornamented bird species (residuals from a regression of the residual number of species per genus on relative species richness in ornamented genera; see Fig. 2) in relation to mating system of the genus (0 = monogamous, 1 = polygynous, 2 = lekking; Kendall τ = 0.19, n = 67, z = 2.32, P = 0.020).

play may account for some of the residual variation in relative species richness.

The mechanisms that have given rise to an increase in the number of species in taxa with feather ornaments may be of two different kinds. Fisher (1930) hypothesized that female mate preferences and male secondary sexual characters may coevolve to ever more extreme expressions under certain conditions. The Fisherian mechanism may be predicted to be particularly powerful in situations in which there is extreme skew in male mating success, such as in species with a lek mating system, simply because the advantage of pure male attractiveness will be particularly great under circumstances in which the potential mating success of males is very high. Sexual selection arising from female mating preferences for male viability indicators may also result in speciation (Schluter and Price 1993). For example, contrasts between male coloration and the color of habitats can give rise to dramatic evolutionary divergence between populations in both the male trait and the female preference (Schluter and Price 1993). Although it is inherently difficult to distinguish between the two models of speciation by sexual selection, they differ in that the Fisherian mechanism is more important when there is extreme skew in male mating success, whereas the viability-indicator mechanism is least plausible in mating systems with extreme skew in male mating success because intense directional selection supposed to exist in lekking species will deplete additive genetic variance in viability (Charlesworth 1987; Burt 1995). Consistent with the Fisher mechanism, we found a greater residual number of ornamented species in genera with a lekking mating system as compared to genera with polygynous or monogamous systems (Fig. 3).

The validity of this comparison is based on the assumption that the social mating system also reflects the genetic mating system, which is not necessarily the case. However, a comparative analysis of extrapair paternity (which results in an increase in the variance in male reproductive success; review in Møller 1998) in relation to the social mating system of birds revealed no difference in extrapair paternity between monogamous and polygynous birds (Møller and Birkhead 1994). The fact that we classified species as monogamous or polygynous based on an arbitrary criterion that more or less than 5% of males mate with more than one female may undermine confidence in our conclusions. However, this traditionally used criterion is unlikely to have caused any significant bias because only six species were classified as polygynous. Further, until more of the species listed in Appendix 2 are well studied, it will not be possible to analyze the relationship between species richness and the proportion of males having more than a single mate. In conclusion, our analyses suggest that the there is a positive relationship between mating skew as determined from the social mating system and residual number of ornamented species. This finding implies that the Fisherian mechanism of sexual selection is one of the factors that has contributed to the increase in species richness under sexual selection.

Males of closely related species often differ greatly in secondary sexual characteristics, whereas females are frequently very similar in their appearance across the same range of species (Darwin 1871). Such differences in the appearance of males have been attributed to the divergence in female mating preferences (West-Eberhard 1983; Houde and Endler 1990; M. Andersson 1994), with differences in appearance of males resulting in premating reproductive isolation (Mayr 1942, 1963). Our comparative analyses suggested that ornamented species on average had a relatively larger number of subspecies than did closely related species without ornaments. Although the existence of subspecies as biological entities is disputed (Mayr 1942, 1963), there is clear evidence that populations differ in appearance. For example, many, if not most, subspecies of birds can be distinguished and identified in the field by competent ornithologists. Such incipient morphological differentiation within species can be considered to be an initial step in the phenotypic divergence among allopatric populations (Houde and Endler 1990).

If sexual selection increases the rate of speciation giving rise to more ornamented species, this process is obviously not the only one affecting species richness because not all species currently have extravagant secondary sexual characters. The relationship between sexual selection and extinction was discussed already by Fisher (1930), and sexual selection may in theory result in severe reductions in the mean fitness of a population. Subsequent modeling has demonstrated that this effect of selection load may be an important determinant of extinction (Tanaka 1996). The viability-indicator mechanism cannot counter this effect because an increase in the magnitude of indirect fitness benefits acquired by choosy females will be offset by a reduction in male viability caused by ornamentation. For example, excess mortality in male birds compared to that of females is directly related to the degree of exaggeration of male coloration (Promislow et al. 1992, 1994; Owens and Bennett 1994). Analyses of extinction in mammalian fossil lineages (McLain 1993) demonstrate that lineages become larger during time and subsequently increase their risk of extinction. Similarly, analyses of the introduction success of bird species on oceanic islands in relation to sexual dichromatism revealed that dichromatic species ran a greater risk of extinction than monochromatic species, even when taking a number of potentially confounding variables such as the number of individuals introduced into account (McLain et al. 1995; Sorci et al. 1998). The association between sexual selection and speciation investigated in the present study thus can be considered to be an underestimate of the real effect simply because differential extinction of sexually selected species will tend to reduce species richness in highly sexually selected lineages.

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APPENDIX 1

Sources of information used for identifying feather ornaments in birds and the ecological variables of the bird species considered in this study.

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APPENDIX 2

Number of subspecies, mating system, and breeding range of avian sister species with (the first species in each pair) and without (the second species) feather ornaments. When the nonornamented species belongs to a genus with some ornamented species, we have chosen a different nonornamented sister genus for the comparative analyses (the third taxon listed for some groups). The source for the number of species per genus and the number of subspecies per species is Howard and Moore (1991). The reference numbers correspond to publications listed in Appendix 1.

Species (genus)	No. of species in the genus (no. of ornamented species)	No. of subspecies	Mating system	Breeding range (degrees)	References
Podiceps cristatus	11 (1)				
Podiceps dominicus	—	3	monogamous	113	16, 44, 66
Podilymbus	2	5	monogamous	60	23, 44, 102
Anas falcata	37 (8)				
Anas strepera	—	1	monogamous	22	9, 44, 47
Malacorhynchus	1	1	monogamous	33	16, 47, 72
Anas platyrhyncos	—	7	monogamous	41	16, 23, 47
Anas rubripes	—	1	monogamous	28	44, 47, 72
Aythya fuligula	12 (3)				
Aythya marila	—	1	monogamous	27	16, 44, 47
Netta	3	3	monogamous	25	16, 47, 72
Clangula hymelias	1 (1)	1	monogamous	31	16, 47, 72
Melanitta nigra	3	2	monogamous	27	16, 47, 72
Tetrao tetrix	4 (2)	7	lekking	28	16, 49, 58
Lagopus leucurus	3	5	monogamous	30	8, 44, 49
Lophortyx californica	3 (3)				
Colinus virginianus	—	6	monogamous	23	23, 44, 52
Rhynchortyx	1	18	monogamous	29	23, 44, 52
Rollulus rouloul	1 (1)	1	monogamous	18	44, 52, 63
Ptilopachus petrosus	1	5	monogamous	14	10, 44, 52
Gallus gallus	4 (4)	5	polygynous	42	18, 44, 50
Bambusicola fytchii	2	2	monogamous	9	1, 44, 52
Phasianus colchicus	2 (2)				
Lophura inornata	—	31	polygynous	32	16, 18, 50
Coturnix	8	2	—	10	18, 44, 50
Pavo cristatus	2 (2)	1	lekking	28	18, 44, 50
Galloperdix spadicea	3	3	monogamous	17	1, 44, 52
Otis tarda	1 (1)				
Neotis ludwigi	—	3	lekking	20	16, 53, 54
Eurypgya	1	1	polygynous	17	10, 33, 53
Hydrophasianus chirurgus	1 (1)	1	polyandrous	37	1, 40, 63
Metopidius indicus	1	1	polyandrous	38	1, 40, 63
Vanellus vanellus	23 (2)				
Vanellus lugubris	—	1	monogamous	11	16, 40, 48
Pluvialis	5	1	monogamous	40	10, 40, 48
Philomachus pugnax	1 (1)	1	lekking	24	16, 40, 54
Tryngytes subruficollis	1	1	lekking	10	23, 40, 59
Syrrhaptes paradoxus	2 (2)				
Pterocles orientalis	—	1	monogamous	14	16, 28, 53
Actophilornis	2	3	monogamous	23	1, 16, 53
Treron apicauda	23 (1)				
Treron fulvicollis	—	3	monogamous	13	1, 35, 36
Ptilinopus	49	4	monogamous	24	35, 56, 63
Psittacula longicauda	13 (13)	5	monogamous	21	29, 56, 63
Loriculus vernalis	11	1	monogamous	20	1, 29, 56
Scotornis climacurus	3 (2)	3	monogamous	17	10, 64, 99
Phalaenoptilus nuttallii	1	5	monogamous	32	17, 23, 43
Macrodipteryx longipennis	2 (2)	1	polygynous	14	10, 64, 99
Nyctiphrynus ocellatus	1	3	monogamous	35	68, 77, 90
Hydropsalis brasiliana	2 (2)	2	monogamous	33	82, 83, 90
Caprimulgus carolinensis	50	1	monogamous	17	4, 23, 88
Phaetornis superciliosus	24 (24)	14	lekking	37	43, 54, 90
Threnetes leucurus	4	5	monogamous	21	41, 85, 90

APPENDIX 2. Continued.

Species (genus)	No. of species in the genus (no. of ornamented species)	No. of subspecies	Mating system	Breeding range (degrees)	References
Lophornis ornata	8 (8)	1	polygynous	11	26, 39, 85
Chlorestes notatus	1	3	polygynous	26	26, 41, 90
Trochilus polytmus	1 (1)	2	polygynous	1	7, 21, 106
Polytmus guainumbi	3	3	polygynous	41	26, 41, 90
Topaza pella	2 (2)	4	lekking	8	54, 85, 90
Urochroa bougueri	1	3	polygynous	12	27, 41, 83
Oxypogon guerinii	1 (1)	4	polygynous	7	27, 41, 85
Opisthoprora euryptera	1	1	polygynous	13	27, 41, 83
Aglaiocercus kingi	2 (2)	7	polygynous	29	27, 41, 85
Schistes geoffroyi	1	2	polygynous	28	27, 41, 85
Pharomachrus moccino	5 (5)	2	monogamous	8	43, 77, 107
Temnotrogon roseigaster	1	1	monogamous	2	7, 101, 108
Tanysiptera galatea	8 (1)				
Actenoides monacha	—	15	monogamous	14	3, 14, 31
Melidora	1	3	monogamous	8	31, 109
Coracias abyssinicus	8 (2)				
Coracias naevia	—	1	monogamous	16	10, 31, 99
Eurystomus	4	2	monogamous	43	10, 31, 99
Dinopium javanense	4 (2)				
Picus canus	—	6	monogamous	34	1, 63, 110
Blythipicus	2	11	monogamous	69	16, 63, 110
Pithys albifrons	2 (1)	3	monogamous	14	39, 85, 90
Gymnopithys rufigula	4	3	monogamous	13	39, 85, 90
Ruipcola peruviana	2 (2)	4	lekking	25	41, 85, 98
Lipaugus unirufus	7	2	lekking	19	41, 43, 98
Pipra cornuta	16 (2)				
Pipra erythrocephala	—	1	lekking	9	83, 85, 90
Tryanneutes	2	3	lekking	15	77, 90, 107
Chiroxiphia linearis	4 (3)	2	lekking	7	43, 54, 77
Corapipo leucorrhoa	2	3	lekking	11	41, 54, 77
Tyrannus savana	13 (2)				
Tyrannus tyrannus	—	4	monogamous	62	41, 43, 90
Tyrannopsis	1	1	monogamous	35	23, 41, 88
Anairetes reguloides	5 (5)	3	monogamous	24	27, 55, 57
Inezia subflava	3	5	monogamous	23	41, 85, 90
Menura novaehollandiae	2 (2)	2	lekking	10	6, 76, 97
Atrichornis rufescens	2	1	monogamous	5	6, 62, 96
Eremophila alpestris	2 (2)	41	monogamous	73	16, 23, 41
Eremopterix australis	7	1	monogamous	8	10, 33, 91
Hirundo semirufa	34 (13)				
Hirundo preussi	—	2	monogamous	48	10, 37, 104
Delichon	3	1	monogamous	18	10, 37, 104
Hirundo rustica	—	8	monogamous	52	16, 23, 104
Hirundo rufigula	—	1	monogamous	9	10, 37, 104
Psalidoprocne obscura	9 (7)				
Psalidoprocne nitens	—	1	monogamous	5	10, 37, 104
Phedina	2	2	monogamous	15	10, 37, 104
Dryoscopus sabini	6 (6)	2	—	18	37, 64
Tchagra minuta	6	4	monogamous	35	37, 38, 64
Ptilogonys caudatus	2 (1)	1	monogamous	3	77, 107
Hypocolius ampelinus	1	1	monogamous	13	16, 42, 45
Phainopepla nitens	1 (1)	2	monogamous	19	23, 43, 88
Phainoptila melanoxantha	1	1	monogamous	3	77, 107
Copsychus malabaricus	8 (2)				
Copsychus saularis	—	18	monogamous	39	1, 56, 63
Irania	1	18	monogamous	44	1, 25, 63
Panurus biarmicus	1 (1)				
Paradoxornis gularis	—	3	monogamous	94	16, 25, 28
Conostoma	1	7	—	13	1, 25, 56

APPENDIX 2. Continued.

Species (genus)	No. of species in the genus (no. of ornamented species)	No. of subspecies	Mating system	Breeding range (degrees)	References
Orthotomus sutorius	12 (1)				
Orthotomus atrogularis	—	9	monogamous	44	1, 25, 63
Camaroptera	5	9	monogamous	34	1, 56, 63
Malurus splendens	12 (5)				
Malurus cornatus	—	5	monogamous	14	6, 62, 86
Amytornis	8	2	monogamous	4	6, 62, 86
Terpsiphone viridis	14 (14)	10	monogamous	54	37, 64, 65
Chasiempis sandwichensis	1	5	monogamous	3	5, 67
Nectarinia johnstoni	78 (12)				
Nectarinia notata	—	3	monogamous	20	37, 64[#]
Hypogramma	1	3	—	15	37, 60
Anthochaera carunculata	3 (1)	2	monogamous	12	6, 61, 62
Acanthagenys rufogularis	1	2	monogamous	18	6, 61, 69
Prosthemadera novaeseelandiae	1 (1)	3	monogamous	13	70, 80, 103
Manorina melanophrys	5	1	monogamous	13	6, 61, 62
Melophus lathami	1 (1)	1	monogamous	17	1, 25, 56
Emberiza calandra	38	1	monogamous	31	16, 25, 28
Cardinalis cardinalis	1 (1)	18	monogamous	30	23, 43, 78
Caryothraustes canadensis	3	3	monogamous	32	41, 78, 90
Quiscalus mexicanus	6 (5)	8	polygynous	46	23, 41, 78
Euphagus carolinus	2	2	monogamous	25	2, 23, 88
Erythrura prasina	11 (1)				
Erythrura hyperythra	—	2	monogamous	27	13, 34, 63
Aidemosyne	1	6	monogamous	28	13, 34, 63
Vidua macroura	10 (6)				
Vidua funerea	—	1	lekking	50	37, 54, 64
Parmoptila	2	4	polygynous	47	33, 37, 64
Euplectes jacksoni	16 (8)				
Euplectes hordacea	—	1	lekking	5	37, 54, 64
Quelea	3	2	polygynous	36	33, 37, 64
Aplonis metallica	22 (3)				
Aplonis cantoroides	—	5	monogamous	23	3, 6, 62
Grafisia	1	1	monogamous	12	3, 14, 75
Sturnus unicolor	16 (3)				
Sturnus cineraceus	—	1	monogamous	15	16, 24, 42
Spreo	6	1	monogamous	18	9, 25, 28
Dicrurus paradisaeus	21 (3)				
Dicrurus ludwigii	—	14	monogamous	39	1, 56, 63
Philentoma	2	4	monogamous	49	33, 37, 64
Amblyornis subalaris	4 (3)				
Amblyornis inornatus	—	1	lekking	2	3, 15, 32
Prionodura	1	1	lekking	3	3, 15, 32
Pteridophora alberti	1 (1)	3	lekking	3	3, 15, 32
Manucodia jobiensis	4	2	monogamous	4	3, 15, *
Ptiloris magnificus	3 (3)				
Manucodia ater	—	3	lekking	14	6, 15, 32
Melampitta	2	3	monogamous	12	3, 15, 20
Semioptera wallacei	1 (1)	2	lekking	3	15, 20, 109
Paradigalla brevicauda	2	1	polygynous	5	3, 15, *
Lophorina superba	1 (1)	8	lekking	10	3, 15, 32
Macgregoria pulchra	1	2	monogamous	6	3, 15, 20
Parotia lawesii	4 (4)	2	lekking	5	3, 15, 20
Loboparadisea sericea	1	2	—	4	3, 15, 32
Diphyllodes magnificus	2 (2)	4	lekking	11	3, 15, 32
Loria loriae	1	3	polygynous	5	3, 15, *
Paradisaea rubra	7 (7)	1	lekking	1	15, 20, 32
Lycocorax pyrrhopterus	1	3	monogamous	4	15, 32, 109

[#] M. R. Evans (pers. comm.); * C. B. Frith (pers. comm.).