

Sex-limited expression of ornamental feathers in birds

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Extravagant secondary sexual characters show sexual size dimorphism in some species but are completely sex limited in others. Sexual ornamentation has been hypothesized to benefit mainly males through sexual selection, but the costs of secondary sexual characters initially would be experienced by both sexes. The evolution of sexual size dimorphism of ornaments and, eventually, the complete sex-limited expression of these characters, will depend on the effects of sexual and natural selection on the two sexes. A phylogenetic analysis controlling for similarities due to common ancestry of 60 independent evolutionary origins of feather ornamentation in birds was used to investigate ecological factors correlated with sexual size dimorphism and sex-limited expression of secondary sexual characters. When the size of an ornament is large relative to body size, the trait will be particularly costly for females, resulting in selection for increased sexual size dimorphism of the ornament. Indeed, sexual size dimorphism of ornaments was positively related to the relative size of male ornaments but was unrelated to relative size of female ornaments. Species with polygynous and lekking mating systems with little or no male parental care (in particular nest building and incubation) demonstrated sex-limited expression of ornaments as compared to monogamous species. Species with no food provisioning of offspring by the male showed a trend for increased sexual size dimorphism of ornaments. Therefore, large natural selection costs during reproduction imposed by the expression of secondary sexual characters are related to the evolution of sexual size dimorphism of ornaments and eventually their complete loss from females. *Key words:* sex limitation, sexual selection, sexual size dimorphism. [*Behav Ecol* 11:246–259 (2000)]

Sexual selection arises as a consequence of variation in mating success, being nonrandomly related to phenotypic characters that are advantageous during competition for mates (Darwin, 1871). Such characters are termed secondary sexual characters, and two different processes can account for their evolution: intrasexual competition (usually male–male competition) and mate choice (usually female choice of mates) (Andersson, 1994; Darwin, 1871). Observational and experimental evidence suggests that feather ornaments of birds play an important role in female choice, but they are of no or little significance in male–male competition (reviews in Andersson, 1994; Møller, 1994). Female choice is therefore presumed to account for the maintenance of extravagant plumage ornaments in birds.

Feather ornaments of birds are usually large and conspicuous morphological characters, and they are therefore presumably costly to produce and maintain (Andersson, 1994; Møller, 1996). Natural selection costs of ornamentation have been hypothesized to include the costs of production of the ornament, but also may include costs of predation due to increased attraction of predators (e.g., Endler, 1980; Götmark, 1993; Magnhagen, 1991; Møller and Nielsen, 1997), costs of a suppressed immune system (e.g., Folstad and Karter, 1992; Saino and Møller, 1996), and the physiological costs of carrying an extravagant exaggerated character (e.g., Saino et al., 1997; but see Cuervo et al., 1996b). Although these costs have only been studied in males, partial expression of male traits by females is also likely to be costly.

The occurrence of ornamental feathers is often limited to

the male sex, but a number of species show partial expression of secondary sexual characters in females. The degree of sex limitation of ornamental feathers can be classified as females not expressing ornaments (total sex limitation) or females with shorter extravagant ornamental feathers than males (partial sex limitation). Among species with partial sex limitation, we can find different degrees of sexual size dimorphism of ornaments. Whether ornaments are expressed in females, and the degree of sexual size dimorphism of these characters, may depend on the costs to females of developing and carrying an exaggerated trait. The evolution of sexual size dimorphism is presumably a process governed by the differential effects of selection on individuals of the two sexes. Phenotypic characters often have strongly positive genetic correlations between the sexes (Falconer, 1989), and this is also the case for secondary sexual characters expressed in both sexes (Møller, 1993; Wilkinson, 1993). Any selection for increased size of a character among individuals of one sex will therefore result in a correlated response to selection among individuals of the other sex. However, changes of genetic correlations are presumably caused by oppositely directed selection pressures in the two sexes (Lande and Arnold, 1985). The average phenotype of the two sexes together would evolve on a fast time scale, while sexual dimorphism would evolve on a slow time scale. For a single character in each sex, the ratio of the slow time scale to the fast time scale would be $(1 + \gamma)/(1 - \gamma)$, where γ is the additive genetic correlation between the sexes (Lande, 1980). The rate of evolution of sexual dimorphism when γ is high (≥ 0.9) may be one or more orders of magnitude slower than that for the average phenotype in a population. The evolution of sexual size dimorphism initially proceeds slowly, but would eventually increase in speed as the genetic correlation is reduced due to genetic modifiers that change the expression of the character in females (Lande and Arnold, 1985). As the female trait eventually is reduced in

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size, the natural selection costs of its expression would also be reduced. Vestigial forms of a male trait may therefore be expressed in females for an extended period of time (Lande and Arnold, 1985).

Although the theory of evolution of sexual size dimorphism hypothesized above is relatively well understood (e.g., Lande, 1980; Lande and Arnold, 1985), there are few empirical tests available. A comparative study of sex differences in mortality rates of birds revealed a positive relationship between sexual dichromatism and mortality (Promislow et al., 1992). However, a subsequent study based on a larger data set provided a less clear-cut result, with parental care rather than sexual dichromatism accounting for sex differences in mortality among adult birds (Owens and Bennett, 1994). A study of sex differences in mortality in waterfowl with relatively similar ecology, and a complete absence of male parental care, demonstrated a positive relationship between male biased mortality and sexual dichromatism, thus ruling out any confounding influence of male parental care (Promislow et al., 1994). Such sex-biased mortality is assumed to be due to sex differences in exposure to predators during reproduction. A comparative analysis of passerines and sex roles in parental care showed that dull female plumage was associated with nest sites with a high risk of predation on females during incubation and brooding, whereas this was not the case for the brightness of male plumage (Martin and Badyaev, 1996). Furthermore, Badyaev (1997) has recently shown that both male and female coloration correlates with clutch size in the cardueline finches, but the signs of the correlation differ for the sexes: males were brighter in species with large clutches, but females of these species were less bright. Irwin (1994) found that plumage dichromatism in Icterinae was greater in polygynous species than in monogamous ones, in particular due to changes in female plumage brightness.

While all the studies mentioned above have focused on sexual dichromatism in a single avian group, we have studied sexual size dimorphism of ornaments across all avian families. We tested for the ecological correlates of sexual size dimorphism and complete sex-limited expression of secondary sexual characters using birds with extravagant feather ornaments as a model system. Our predictions are based on the assumption that females do not benefit from secondary sexual characters, or, at least, they benefit from these characters through sexual selection to a much smaller degree than males. However, both sexes are impaired by ornaments through natural selection. In males the costs of ornaments through natural selection can be balanced by their sexual selection benefits. In females, however, costs of ornaments have little or no compensation, and ornaments will tend to diminish. Consequently, the larger the natural selection costs imposed, the larger the degree of sex limitation of ornaments.

We tested four predictions concerning sexual size dimorphism and sex-limited expression of secondary sexual characters. First, the expression of ornaments in females will depend on the size of the secondary sexual character in males because only relatively large characters will be sufficiently costly to select for sex-limited expression. In this prediction we are assuming that, everything else being equal, species with the largest ornaments also incur the largest costs due to ornamentation. These natural selection costs due to ornamentation might be balanced by sexual selection benefits in males, but not in females. Obviously, species differing in ornament length may also differ in ecology or life history that affect the cost of ornaments.

Second, the evolution of sex-limited expression of ornaments will depend on the mating system because a more extreme skew in male mating success from monogamy over polygyny to lekking is presumably associated with more intense

sexual selection for ornament expression in males (Darwin, 1871; Møller and Pomiankowski, 1993). As a consequence, there would be more intense natural selection against expression of the male trait in females due to the increased role of the female in reproduction. If females provide most or all parental care, as in polygynous and lekking species (Darwin, 1871; Orians, 1969), there is particularly strong natural selection against expression of secondary sexual characters in females, for example, due to predation during reproduction (Martin and Badyaev, 1996; Promislow et al., 1992, 1994). We tested for the importance of different parental duties on the evolution of sex limitation of extravagant secondary sexual characters.

Third, migration is a widespread but energetically costly activity in birds. The costs of expression of secondary sexual characters are likely to be elevated in migratory as compared to resident species, simply due to the costs of flight with extravagant, aerodynamically non-functional feathers, and this should affect the sex limited expression of secondary sexual characters (Balmford et al., 1993). According to our predictions large natural selection costs due to ornamentation would be related to a large degree of sex limitation of ornaments. Therefore, migrants are expected to show greater sexual size dimorphism of ornaments than nonmigrants. Fourth, the predictability of food and the foraging mode may potentially also play important roles in the evolution of sex limitation of ornaments. The relative amount of the energy budget spent on locomotion may be temporally highly variable if the food resource is unpredictable in time or space. A large degree of variation in the costs of locomotion will put upper limits to the degree of ornamentation in both sexes, but mainly in females. Unpredictable food such as animal food and expensive foraging modes such as aerial insectivory should be related to a higher degree of sex limitation than more predictable food and less costly foraging modes.

We emphasize that each prediction (i.e., the relationship between the degree of sex-limited expression of ornaments and the ecological variables) is based on an assumption of everything else being equal. For example, aerial feeding would be related to large degrees of sex limitation of ornaments as compared to ground foraging if the two groups of species do not differ in other variables (relative ornament size, male provisioning, migratory habits). Obviously, all the variables we are studying might be related to one another. The four predictions were investigated for a number of evolutionary events of extravagant feather ornamentation in birds using a phylogenetic approach.

METHODS

Definition of feather ornaments

We have identified independent evolutionary events of feather ornamentation in extant birds. We excluded cases of extravagant feather characters in both sexes when there was no sexual size dimorphism, although mutual sexual selection may account for such exaggerated monomorphism (Jones and Hunter, 1993). We admit that more studies have to be performed before we can dismiss mutual sexual selection as an important factor in the evolution of exaggerated sexual size monomorphism. For the time being we assume that extravagant sexually size dimorphic traits are associated with sexual selection, as demonstrated by numerous observational and experimental studies (see Andersson, 1994). Sexual size monomorphism was not the subject of the present study. Furthermore, we have not considered either feather colors or naked skin patches in the present study.

Sexually size-dimorphic traits were considered to qualify as

secondary sexual characters if there was a sex difference in their absolute size of at least 5% because previous studies have considered this cut-off point for dimorphism (Höglund, 1989; Höglund and Sillén-Tullberg, 1994; Oakes, 1992). Species investigated were recorded from extensive searches of the literature (see Appendix) and major European museum collections (see Acknowledgment). Representative species of all independent evolutionary events of extravagant feather ornamentation (see "Phylogenetic information" below) that were suggested to be sexually size dimorphic in a feather character in the consulted literature were investigated by measuring 10 males and 10 females, although a few species could not be measured due to their rarity and hence a shortage of specimens in the museum collections visited. A total of 82 species investigated resulted in 12 being considered to be sexually size monomorphic, according to the criterion stated above, and 70 sexually dimorphic in ornament size. Because the phylogeny was not known for all species, we could only include 60 of these species in our analyses; 49 out of these 60 species were classified as showing partial sex limitation of ornaments. We could not measure female ornaments for *Pteridophora alberti* (female specimens were not available in the museum collections visited), and *Rollulus rouloul* (female specimens had ornamental feathers in a poor state). These two species were classified as showing partial sex limitation of ornaments because the literature (see references in the Appendix) clearly showed that females were ornamented, but with much smaller ornaments than males. The remaining 11 species with a feather character only being expressed in males were all considered to be sexually size dimorphic with complete sex limitation of the character. We could not measure female specimens for *Pipra cornuta* (they were unavailable in the museum collections visited), but this species was classified as showing total sex limitation of ornaments because the literature (see references in Appendix) clearly showed that males were ornamented but females were not. Female feathers were considered ornaments when they were larger than expected for a particular feather tract—that is, longer than ordinary feathers, as compared with other feathers in the same species or equivalent feathers in closely related species.

The degree of dimorphism of ornaments $\{[(\text{male size} - \text{female size}) / (\text{female size})] \times 100\}$ among species with partial sex limitation of ornament expression ranged from 5.0% to 450.9%, with a mean value of 67.9% (SE = 14.0, $n = 47$ species). Moreover, ornament dimorphism was not due to a general difference in body size between sexes because in the 43 species with males showing longer wings than females, ornament dimorphism (as defined above) was on average 12.2 times larger than wing dimorphism (SE = 2.8), and always more than 1.5 times larger.

Phylogenetic information

In this study we used the phylogeny of Sibley and Ahlquist (1990) to identify evolutionarily independent events of extravagant feather ornamentation in birds. Despite much criticism, the phylogeny of Sibley and Ahlquist (1990) has been verified in a large number of cases by independent phylogenetic studies (Bleiweiss et al., 1995; Harshman, 1994; Mooers and Cotgreave, 1994; Sibley, 1994). For the family Hirundinidae, information on intrafamilial phylogenetic relationships is available that allowed discrimination of the number of intrafamilial independent evolutionary events of extravagant feather ornaments (Sheldon and Winkler, 1993). We have only used phylogenetic information based on DNA-DNA hybridization (Sheldon and Winkler, 1993; Sibley and Ahlquist, 1990).

Feather ornamentation has evolved independently a large number of times. If no other phylogenetic 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 counted as evolutionarily independent 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 independent evolutionary events, since these traits were obviously developmentally and morphologically independent. If more than a single ornamented species was available within a taxon, we exclusively used abundance as the criterion for choice of species to be used in our analysis, due to more ecological information being available for abundant species.

We have not found resolved phylogenies for all 70 species classified as ornamented. Because some methods of comparative analysis (Pagel, 1994, 1997) cannot deal with polytomies (node with more than two descendant nodes), we have excluded from our analyses 10 of the 70 species in order to achieve a perfectly bifurcated phylogeny. We have in these cases maximized the number of contrasts. Every branch in the phylogeny was considered to have the same length. All 60 species included in the study and their phylogenetic relationships are shown in Figure 1.

Ecological variables

For all bird species considered, we made an extensive search in the literature for information concerning mating system, parental care, diet, migration, and additional natural history variables potentially influencing the evolution of sexual size dimorphism and sex limitation of feather ornaments. These references are listed in the Appendix. Four different mating systems have been considered: (1) social monogamy ($n = 38$ species) if single males and single females associated for reproduction, (2) polygyny ($n = 6$) if at least 5% of the males in one population were associated with more than a single female for reproduction, (3) polyandry ($n = 1$) if at least 5% of the females were associated with more than a single male for reproduction, and (4) lekking ($n = 15$) if males aggregated at communal display grounds where females arrived to make their mate choice. Category 1 was considered monogamy and categories 2–4 were considered polygamy throughout the analyses. Male parental care was divided into three categories: nest building, incubation, and feeding of offspring. Species were classified as having no or some male contribution for each of the three categories (21 species with male nest building, 31 without; 16 species with male incubation, 37 without; 26 species with male young provisioning, 26 without).

Our data show that social mating system is significantly related to male nest building [omnibus test, likelihood ratio (LR) = 15.38, p (simulation) < .01], male incubation (LR = 18.86, $p < .01$), and provisioning of young by the male [LR = 34.69, $p < .01$; general method of comparative analysis for discrete variables (Pagel, 1994, 1997); see "Statistical procedures" below]. Species with a high skew in male mating success showed less male contribution to parental care.

Bird species were classified according to their migratory regime as migrants ($n = 4$ species), partial migrants ($n = 18$), or residents ($n = 37$) depending on whether there was no overlap, some overlap, or complete overlap between breeding and nonbreeding ranges due to seasonal movements. Diet was classified in three categories: mainly animal food ($n = 23$ species), mainly vegetable food (excluding fruit) ($n = 23$), and mainly fruit ($n = 13$). Omnivorous species were classified as relying on animal or vegetable food depending on the most important contribution to the diet. For our analyses we pooled vegetable and fruit eaters. The common mode of locomotion while foraging was classified as aerial ($n = 13$ spe-

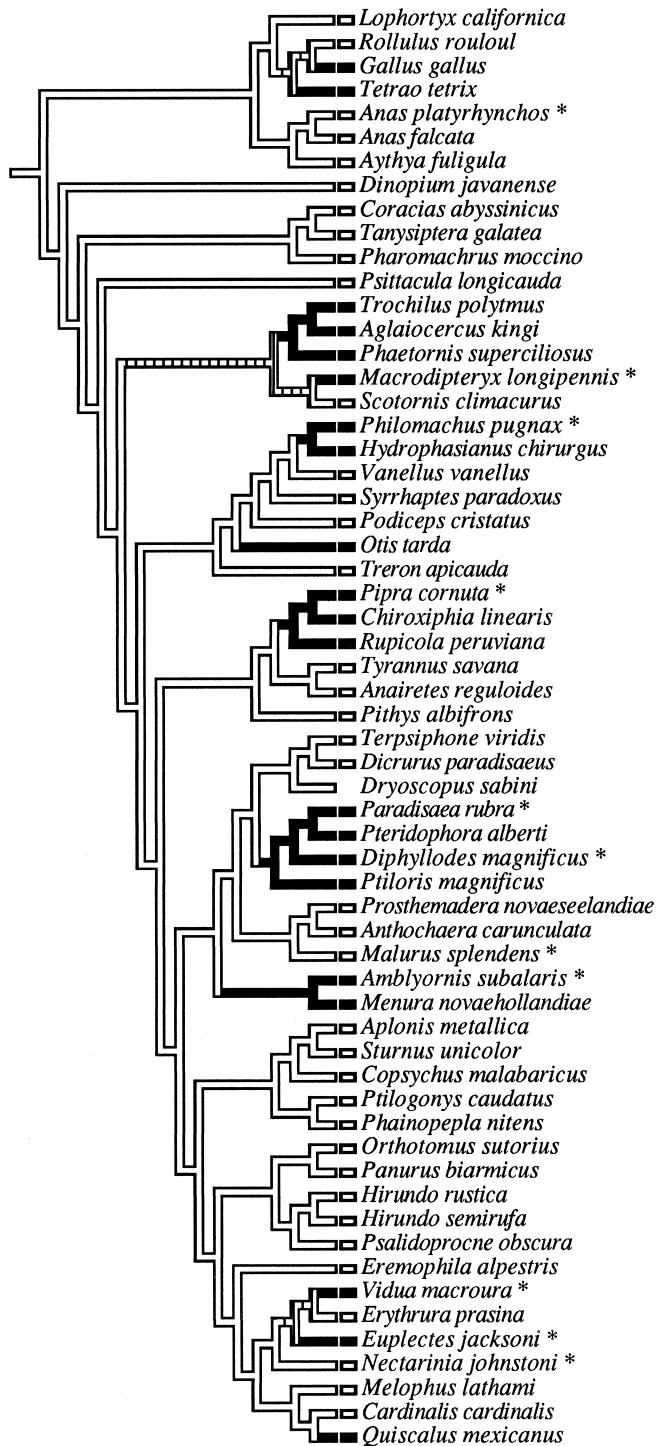


Figure 1
Phylogenetic relationships among the 60 ornamental bird species included in this study based on Sibley and Ahlquist (1990) and Sheldon and Winkler (1993). Open branches indicate socially monogamous taxa. Solid branches indicate polygynous, polyandrous, or lekking taxa. Equivocal branches are striped. *Total sex limitation of the expression of ornaments.

cies), diving ($n = 2$), swimming ($n = 2$), perching ($n = 22$), and ground foragers ($n = 20$). Aerial foragers obtain all their food from pursuing food (usually invertebrates) in flight. Divers pursue food while diving. Because our emphasis was on the consequences of costly behavior on the evolution of sex-

limited expression of extravagant ornaments, for the analyses we separated species with costly foraging modes (aerial, diving) from the others (swimming, perching, ground foragers). Ornament categories and ecological variables of all species are listed in the Appendix.

Measurement of specimens

For most species we measured 10 males and 10 females, although in some cases (see Appendix) it was impossible to obtain this number of adult specimens in breeding plumage and good feather condition. Individuals with broken or worn feathers were excluded. The mean number of specimens per species and sex was 9.9 ± 0.5 SD, with a minimum value of 7. Specimens were chosen in the order they appeared in the collections, which prevents any involuntary bias in sampling. We were especially careful in excluding specimens in molt by checking all specimens for the presence of feather quills. If ornaments only appear during part of the year, only specimens from that period were considered. For each species we measured the length of right and left flattened wing and the maximum length of right and left sides of ornaments to the nearest millimeter using a ruler. Measurements were made according to Svensson (1984). The size of phenotypic characters of specimens was simply the mean value of the right and the left character. Summary statistics for all measurements are given in the Appendix.

All specimens of each species measured belonged to the same subspecies and, when possible, to the same population. In *Hydrophasianus chirurgus*, females were more ornamented than males due to the polyandrous mating system, and female measurements were therefore included in the analyses as "male measurements" and male measurements as "female measurements."

We assessed the repeatabilities of our measurements in four species (*Anas platyrhynchos*, *Hirundo rustica*, *Sturnus unicolor*, and *Vanellus vanellus*) with different kinds of ornaments and different body sizes by measuring the same individuals (right and left sides of wings and ornamental feathers) on 2 different days without knowledge of the results obtained on the first day. Repeatabilities (Becker, 1984) ranged from 0.989 to 0.999. In all 16 cases $F \geq 188.8$ and $p < .0001$. For *Hirundo rustica* and *Sturnus unicolor* $df = 29,30$; for *Anas platyrhynchos* $df = 27,28$; for *Vanellus vanellus* $df = 30,31$ (wing feathers) or $df = 27,28$ (crest feathers). Repeatabilities were large, suggesting that our measurements were sufficiently precise to allow quantitative analyses.

Statistical procedures

We made two separate types of analyses to investigate the possible relationship between sex-limited expression of ornaments and different ecological variables. First, among species with partial sex limitation of ornaments we investigated the relationship between the degree of sexual size dimorphism of ornaments and the ecological variables. Second, we compared the group of species with total sex limitation with the group of species with partial sex limitation with respect to the ecological variables. These two types of analyses allowed assessment of ecological variables being associated with differences in sexual size dimorphism of ornaments as well as differences in ecological variables being related to total sex limitation of ornaments. Obviously, if particular ecological conditions affect the evolution of sexual size dimorphism of ornaments, we should expect the same conditions eventually to give rise to complete sex limitation.

Relative size of ornaments was calculated for each sex using the statistical software CAIC to control for similarity due to

common descent (Purvis and Rambaut, 1995). First, we analyzed $\log_{10}$ -transformed ornament length and $\log_{10}$ -transformed wing length together, using the Crunch procedure, and regressed the contrasts (independent standardized linear contrasts) of the dependent variable (ornament length) on the contrasts of the independent variable (wing length) through the origin (Purvis and Rambaut, 1995). The expected value of the slope equals the true relation between the two variables in the absence of phylogenetic effects (Pagel, 1993). Next, we fitted the slope of this regression to the original $\log_{10}$ -transformed wing data and calculated the expected values of $\log_{10}$ -transformed ornaments. Original $\log_{10}$ -transformed ornament data minus the expected values will give us the residuals of the regression. These residuals represent relative ornament length independent of body size for each sex. We used wing length instead of body mass as a measure of body size because insufficient body mass data were available in the literature.

To calculate sexual size dimorphism of ornaments, we analyzed relative size of male ornament and relative size of female ornament again using the Crunch procedure and regressed the contrasts of male ornament on the contrasts of female ornament through the origin. As above, we fitted the slope of this regression to the original relative size of ornaments and calculated residuals from this line. We have used these residuals as a measure of sexual size dimorphism of ornaments. Sexual size dimorphism of ornaments was only calculated for species where both males and females had ornaments. Our method of calculating sexual size dimorphism of ornaments not only controls for similarities due to common descent, but also for possible allometric relationships between the size of the character in the two sexes (Ranta et al., 1994; Rensch, 1950, 1959). Previous empirical studies have neglected this allometry effect when investigating the relationship between the ratio of male size to female size and the size of females, for example in reptiles (e.g., Shine, 1991), birds (e.g., Höglund, 1989; Møller, 1986; Payne, 1984), or mammals (e.g., Clutton-Brock et al., 1977; Kappeler, 1991).

To investigate the relationship between the degree of sexual size dimorphism of ornaments and the ecological variables, we used the Brunch procedure of the program CAIC (Purvis and Rambaut, 1995). This procedure allows tests of whether the evolution of one continuous variable (sexual size dimorphism of ornaments) is related to the evolution of one categorical variable (all our ecological variables). We have reduced all the ecological variables to have only two states. A positive contrast for sexual size dimorphism of ornaments at a node means that this variable is varying in the same direction as the categorical variable. Under the null hypothesis that evolution in the continuous variable has not been linked to the evolution of the categorical variable, we should expect half the contrasts in the dependent variable to be positive and half negative and the mean value of the contrasts to be zero. We have tested this null hypothesis using one sample *t* tests on the mean contrasts for each analysis. For example, if polygynous species are coded "1" and monogamous species "0," a positive mean value would imply that sexual size dimorphism of ornaments tends to be larger in polygynous species and a negative value that sexual size dimorphism of ornaments tends to be larger in monogamous species.

To investigate the total or partial sex limitation of ornaments (a categorical variable) with respect to the ecological variables (also categorical variables), we used the general method of comparative analysis for discrete variables proposed by Pagel (1994, 1997). Pagel's method develops maximum likelihood estimates of the rates of change in the discrete characters and tests the hypothesis of their correlated evolution without relying on reconstructions of the ancestral

character state (Pagel, 1994). A likelihood ratio test statistic (omnibus test) is used to discriminate between two models that are fitted to the data: one allowing only for independent evolution of the two characters (four parameter model), the other involving correlated evolution (eight parameter model). The significance of this likelihood ratio test is assessed using Monte Carlo simulations. Tests of specific directional hypotheses can also be made. These can include tests of whether changes in one variable are more or less likely given the state of the other (contingent changes test), and tests of the temporal ordering and direction of changes (temporal order test). These hypotheses are tested by forcing certain parameters (q_{ij}) in the matrix of transition probabilities to take the same value and fitting that model to the data by maximum likelihood. This model (seven-parameter model) is then compared to the model of correlated evolution (eight-parameter model) by means of a likelihood ratio test. Likelihood ratios will be asymptotically distributed as χ^2 with 1 df (see Pagel, 1994, 1997). It is also possible to force each parameter of the model to zero and compare the models obtained in each case to the full model of dependent evolution (i.e., the eight parameter model). This allows one to construct a flow diagram of evolutionary changes. Again, every variable has only two states, and we have assumed a model of punctuated evolution; that is, every branch in the phylogeny is the same length.

Statistical tests were performed according to Sokal and Rohlf (1995) and Zar (1984). All tests are two-tailed and the level of significance is 5%.

RESULTS

Ecology and sexual size dimorphism of ornaments

The first series of analyses determined the relationship between sexual size dimorphism of ornaments (only in species with partial sex-limited expression of ornaments) and the ecological factors. Sexual size dimorphism of ornaments was positively related to the relative size of male ornaments [Figure 2; $F = 8.99$, $df = 1,45$, $r^2 = .17$, $p = .0044$, slope (SE) = 0.167 (0.056)]. However, sexual size dimorphism of ornaments was far from significantly related to the relative size of female ornaments [$F = 0.00$, $df = 1,45$, $r^2 = .00$, slope = -0.0002 (0.0610)]. Moreover, the difference between the slopes of the two regressions was marginally significant ($t = 2.022$, $df = 44$, $p = .0496$).

Our analyses based on standardized linear contrasts did not show any significant difference in sexual size dimorphism of ornaments between socially monogamous and polygynous/lekking species [mean contrast (SE) = 0.032 (0.025), $t = 1.29$, $df = 7$]. No significant differences in sexual size dimorphism were found for incubation [mean contrast = -0.014 (0.019), $t = -.75$, $df = 11$] or nest building by males [mean contrast = -0.020 (0.023), $t = -0.88$, $df = 10$]. However, sexual size dimorphism of ornaments was slightly less in species in which males fed the young as compared to those in which they did not feed [mean contrast = -0.037 (0.016), $t = -2.26$, $df = 8$, $p = .054$].

We found no significant relationship between sexual size dimorphism of ornaments and migration. We used two approaches: first, we combined migratory and partially migratory species [mean contrast (SE) = 0.012 (0.024), $t = .49$, $df = 11$], and second, we combined resident and partially migratory species (no test possible because there were only two independent contrasts). Neither diet [mean contrast = 0.027 (0.029), $t = 0.92$, $df = 11$] nor foraging mode [mean contrast = 0.018 (0.028), $t = 0.64$, $df = 6$] were significantly related to sexual size dimorphism of ornaments.

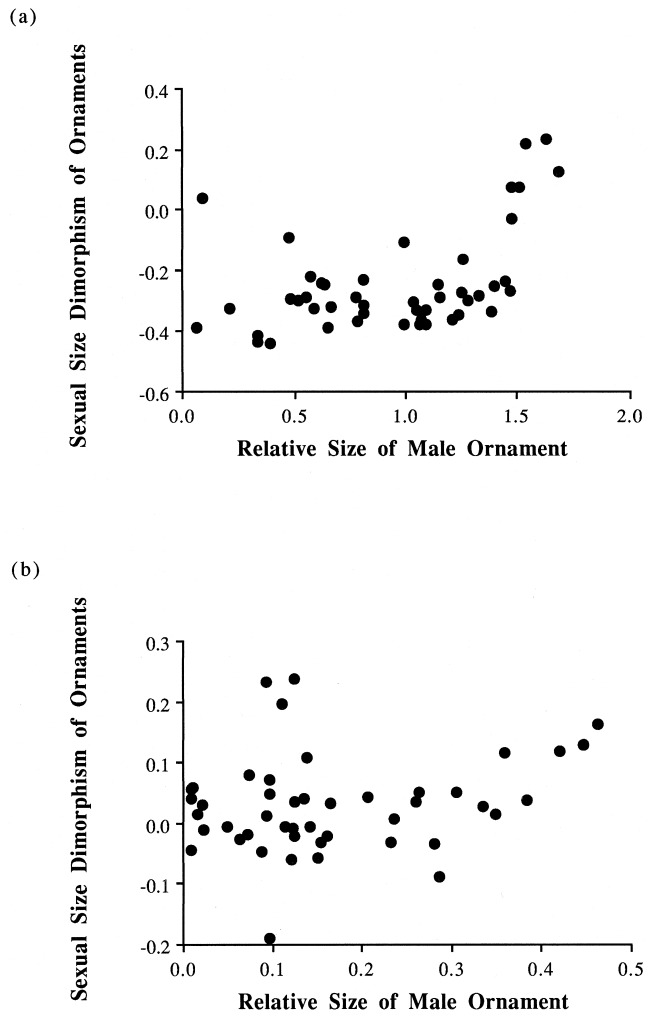


Figure 2
Sexual size dimorphism of ornaments in relation to relative size of male ornaments for birds based on (a) species [$F = 12.00$, $df = 1,46$, $r^2 = .21$, $p = .0012$, slope (SE) = 0.177 (0.051), intercept = -0.411] and (b) statistically independent linear contrasts (analysis parameters in text).

Ecology and relative size of ornaments

Given that sexual size dimorphism of ornaments depends on the relative size of ornaments in the two sexes, it is important to test whether the ecological variables are correlated with relative size of ornaments separately for each sex. For example, lack of correlation between an ecological factor and sexual size dimorphism of ornaments could be due to absence of an effect in either sex, but also by an equal effect of the ecological factor on both sexes. Moreover, although it has been traditionally assumed that sexual dimorphism arises because of changes in male traits, some studies have shown that changes in female traits could be the origin of sexual dichromatism in birds (Björklund, 1991; Burns, 1998; Irwin, 1994; Martin and Badyaev, 1996).

Our analyses based on standardized linear contrasts and including all the species did not show any significant relationship between relative size of male ornaments and mating system [mean contrast (SE) = 0.033 (0.043), $t = 0.78$, $df = 11$], male incubation [mean contrast = -0.021 (0.062), $t = -0.35$, $df = 11$], nest building by males [mean contrast = 0.028 (0.058), $t = 0.48$, $df = 12$], provisioning of young by males

[mean contrast = -0.007 (0.061), $t = -0.12$, $df = 10$], migration [combining migratory and partially migratory species; mean contrast = -0.053 (0.074), $t = -0.71$, $df = 11$], diet [mean contrast = -0.093 (0.059), $t = -1.59$, $df = 13$], or foraging mode [mean contrast = -0.028 (0.093), $t = -0.30$, $df = 6$].

Similarly, relative size of female ornaments, including only species with ornamented females, was not significantly related to mating system [mean contrast (SE) = 0.019 (0.081), $t = 0.23$, $df = 7$], male incubation [mean contrast = -0.001 (0.071), $t = -0.01$, $df = 11$], nest building by males [mean contrast = 0.017 (0.064), $t = 0.27$, $df = 10$], young provisioning by males [mean contrast = -0.0005 (0.082), $t = -0.01$, $df = 8$], migration [combining migratory and partially migratory species; mean contrast = -0.030 (0.079), $t = -0.38$, $df = 11$], diet [mean contrast = -0.117 (0.059), $t = -1.99$, $df = 11$, $p = .072$], or foraging mode (mean contrast = -0.017 (0.098), $t = -0.17$, $df = 6$).

Ecology and sex-limited expression of ornaments

We investigated the relationship between presence of ornamental feathers in females and relative size of male ornaments, mating system, male nest building, male incubation, male provisioning of chicks, migration, diet, and foraging mode.

The relative size of male ornaments was not significantly related to the presence of ornaments in females [mean contrast (SE) = -0.112 (0.080), $t = -1.40$, $df = 9$]. Regarding mating system, females of socially monogamous species showed partial sex limitation of ornaments, and females of polygynous/lekking species showed total sex limitation of ornaments significantly more often than expected by chance [omnibus test, $LR = 8.01$, p (simulation) = $.020$]. None of the two contingent change tests or the four temporal order tests of the relationship between mating system and degree of sex limitation of ornaments (partial or total) was significant ($LR \leq 0.08$). The only significant transitions were (polygyny, partial limitation) $\leftrightarrow$ (polygyny, total limitation) ($LR \geq 3.92$, $p < .05$, in the two cases; Figure 3a). The complete elimination (and the acquisition) of ornamentation in females occurred significantly more often than expected in polygynous/lekking species but not in socially monogamous species.

Sex-limited expression of ornaments was significantly related to nest building and incubation by the male in a similar way: when males participated in parental care, females tended to show partially expressed ornaments, but in the absence of male participation females were significantly more likely to show total limitation of ornaments (nest building: omnibus test, $LR = 13.54$, $p < .01$; incubation: omnibus test, $LR = 9.37$, $p = .015$). None of the contingent change or temporal order tests was significant ($LR \leq 1.74$). In both comparisons, the only significant transitions were (no male care, partial limitation) $\leftrightarrow$ (no male care, total limitation) ($LR \geq 4.54$, $p < .05$, in the four cases; Figure 3b, c). The complete elimination (and the acquisition) of ornamentation in females occurred significantly more often than expected only when males did not invest in parental care. In contrast, sex limitation of ornaments was not significantly related to provisioning of young by the male (omnibus test, $LR = 4.78$). The nonsignificant p value from the simulation (omnibus test) implies that the eight-parameter model does not improve the four-parameter model (see "Statistical procedures"). Because the eight-parameter model will always fit the data better than any seven-parameter model, this means that it is impossible to improve the simple four-parameter model of independent evolution. Therefore, in this case it makes no sense to perform any of the contingent change or temporal order tests.

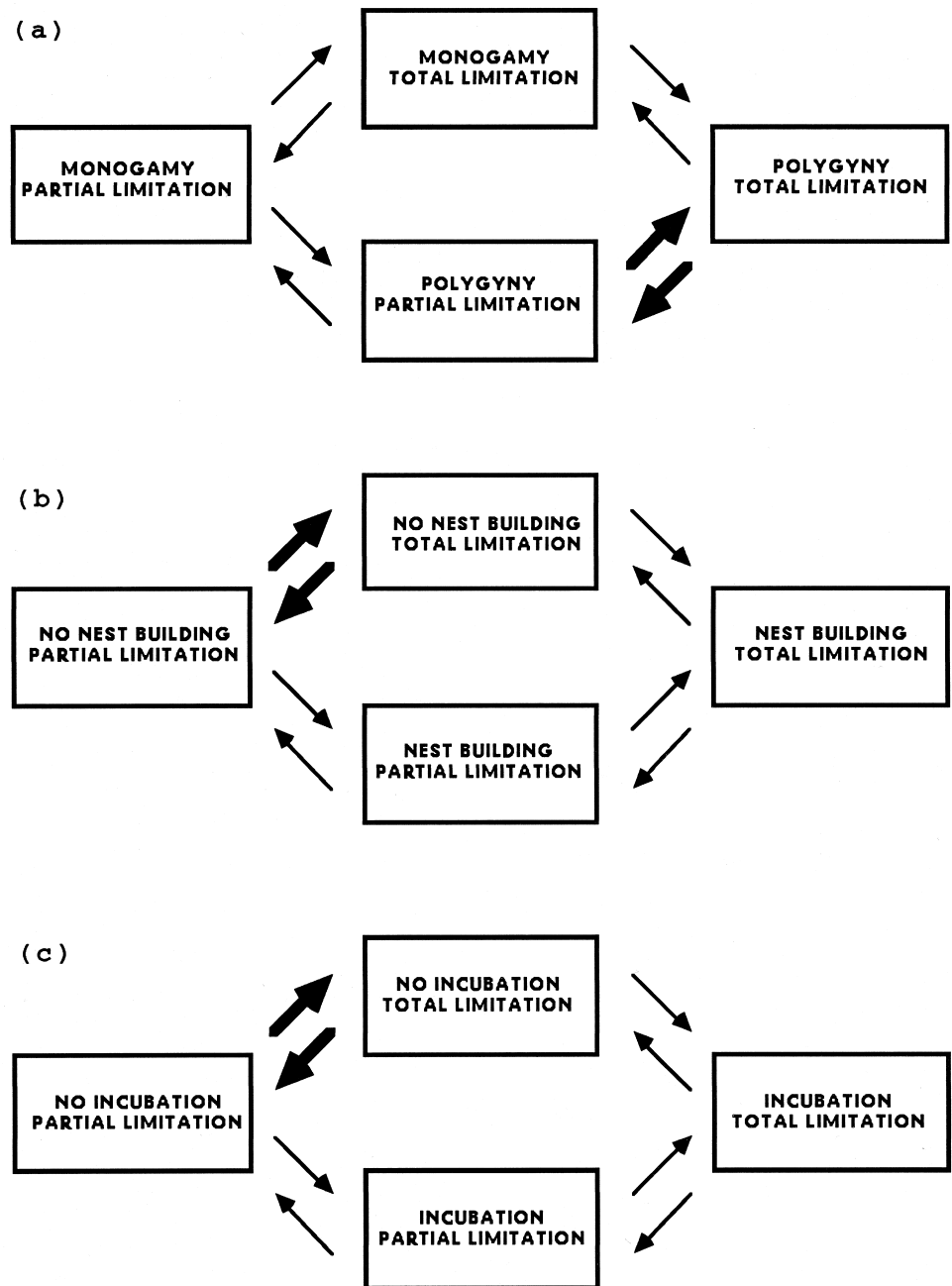


Figure 3

Flow diagrams showing significant pathways (thick arrows) and nonsignificant pathways (thin arrows) involved in the evolution of sex limitation of ornamental feathers in relation to (a) mating system, (b) nest building by the male, and (c) incubation by the male. The arrows represent all possible transitions of one binary character holding the state of the others constant.

Sex limitation of ornamentation was unrelated to migration regime (pooling partially migratory species either with migratory or resident species), diet or foraging mode (omnibus test, $LR \leq 2.38$, ns, in all four cases).

DISCUSSION

Sexual selection may account for the evolution of sexual size dimorphism of ornaments in at least two different ways. First, sexual size dimorphism of ornaments could be the result of female ornaments evolving as a correlated response to selection on males because of a positive genetic correlation between the sexes, but females expressing the male trait to a smaller degree than males because of the large natural selection costs of the trait for females. Sexual size dimorphism of ornaments would in this case result from selection for genetic modifiers that control the expression of the male trait in fe-

males, with simultaneous selection against such modifiers in males (see Introduction). Responses to selection will in this case ultimately depend on the genetic architecture of the species; if there are few genetic modifiers available, positive genetic correlations will prevent the evolution of sexual size dimorphism (e.g., Meagher, 1992).

The second explanation suggests that the female trait is an ornament currently under sexual selection, and different intensities of natural and sexual selection on males and females will give rise to differential expression of the trait in males and females (Cuervo et al., 1996a; Darwin, 1871; Hill, 1993; Jones and Hunter, 1993; Møller, 1993; Muma and Weatherhead, 1989; Trivers, 1972). Empirical evidence suggests that females with the largest secondary sexual characters in species with sexually size-monomorphic characters sometimes experience a mating advantage (Jones and Hunter, 1993), although this is not the case in three sexually dimorphic species

studied so far (Cuervo et al., 1996a; Hill, 1993; Muma and Weatherhead, 1989). Available information thus suggests that sexual dimorphism of ornaments might be a consequence of different selection pressures combined with genetic correlations between the sexes rather than sexual selection increasing the expression of the secondary sexual character in both males and females. Whatever the mechanism may be in different species, the relative strength of natural and sexual selection in the two sexes will give rise to sex-differential expression of ornaments.

A major result of our study relates to the prediction concerning the relationship between the relative size of male secondary sexual characters and the degree of sexual size dimorphism of ornaments. We have studied whether the relative size of male ornaments, after controlling for the effects of allometry and phylogeny, was a reliable predictor of sex limitation of ornaments, based on the assumption that relatively large ornaments are more costly to produce and maintain than small ones. The costs of a relatively large ornament should disproportionately affect females if females have little (or no) advantage of large ornaments through sexual selection that could balance the costs of natural selection. The prediction was tested in two different ways. First, the prediction that the relative size of an ornament should affect the evolution of its sexual size dimorphism was investigated by considering only species with partial expression of the male trait in females. We found a significant positive correlation between sexual size dimorphism of ornaments and relative size of male ornaments (Figure 2). However, the correlation between sexual size dimorphism of ornaments and relative size of female ornaments was far from statistically significant. This correlation was significantly weaker than the same correlation for males, but this result was not a consequence of different amounts of variation in the size of ornaments in the two sexes. First, analyses of the coefficient of variation of ornaments in males and females did not reveal statistically different mean values for males and females (Cuervo and Møller, 2000). Second, the degree of divergence in secondary sexual characters across species was not significantly different in males and females (Cuervo and Møller, 2000). These findings indicate that male ornament size is a much better predictor of sexual size dimorphism of ornaments (and hence sexual limitation of ornaments) than female ornament size. One interpretation of this result is that it is the exaggeration of the male secondary sexual character relative to body size that is causing natural selection costs of the male trait in females. Hence, selection for genetic modifiers that control the expression of the male trait in females should proceed particularly fast in species with extreme exaggeration of male traits. The positive correlation between sexual size dimorphism and relative size of the male trait, but not relative size of the female trait, is the first empirical demonstration that sexual size dimorphism (after controlling for similarities due to common descent and for the allometric relationship between male and female character) increases with increasing size of a phenotypic character in one sex, but not the other (review in Andersson, 1994).

Second, we studied the difference in relative size of secondary sexual characters in species with complete and partial sex-limited expression of ornaments. This difference was far from statistically significant. The second analysis suggests that complete sex-limited expression of male traits is unaffected by the relative size of the secondary sexual character in males and that natural selection costs of the male character for females may differ depending on the ecological context.

An ecological factor generally accepted to be related to the strength of sexual selection in males is the social mating system, with sexual selection supposedly being more intense in

lekking than in polygynous species, and more intense in polygynous than in socially monogamous species (Andersson, 1994; Darwin, 1871; Payne, 1984). Of course, sexual selection may also operate relatively intensely under monogamy (Andersson, 1986; Grafen, 1990; Kirkpatrick et al., 1990; Møller and Birkhead, 1994). The partial or total limitation of the expression of female ornament was found to depend on the social mating system, but the degree of sexual size dimorphism of ornaments among species was not significantly related to mating system. The lack of significance of the latter analysis should be considered with caution because it is based on a small number of contrasts [power analysis (Cohen, 1988), power = 0.22, $d = .065$, $a = 0.05$, $n = 8$]. Ornamented females were mainly found in socially monogamous species, whereas an absence of ornaments mainly occurred in polygynous and lekking species. A previous comparative study of sexual size dimorphism in exaggerated avian tails in relation to sexual selection also found a positive relationship between degree of mating skew as determined by the social mating system and sexual size dimorphism (Winquist and Lemon, 1994).

Parental care is a time- and energy-consuming activity compared to other activities during the annual cycle (Clutton-Brock, 1990). Partial or total limitation of ornaments in females should be affected by the role of males in parental care because a larger male contribution would limit the expression of the secondary sexual character in males and hence reduce the natural selection costs of the male trait in females, and these costs should not be different for males and females with similar sex roles during reproduction (Clutton-Brock and Godfray, 1991; Trivers, 1972; Winkler and Wilkinson, 1988). Therefore, we predicted that sexual size dimorphism of ornaments should be inversely related to male parental care. When males contributed to parenting behavior (building the nest or incubating), species more often only showed partial limitation of ornaments, whereas a complete lack of male parental care was associated with an absence of exaggerated traits in females. The relationship did not reach significance for offspring provisioning by the male. This result is surprising because different kinds of male parental care tend to be positively correlated across species (Lack, 1968; Silver et al., 1985). Moreover, provisioning of young is generally considered to be the most energy-demanding activity of parental care (Clutton-Brock, 1990; Winkler and Wilkinson, 1988), and it should therefore be the most important determinant of sex-limited ornamentation. Among species with ornamented females, sexual size dimorphism of ornaments tended to be greater when males did not feed the young, but we did not find a significant relationship for the other two parenting activities. This finding, however, should be considered with caution because it is based on a small number of contrasts (power analysis; nest building: power = 0.13, $d = 0.38$, $a = 0.05$, $n = 11$; incubation: power = 0.11, $d = 0.30$, $a = 0.05$, $n = 12$; provisioning of young: power = 0.56, $d = 1.07$, $a = 0.05$, $n = 9$). Winquist and Lemon (1994) found that all three male parental care activities were related to sexual size dimorphism of exaggerated tail feathers. Because monogamy is related to a higher proportion of male contribution to parental care (see "Ecological variables"), it is not surprising that the two variables (i.e., social mating system and male parental care) are related to the degree of sex limitation of ornamental feathers in a similar way.

Migration, diet, and foraging mode were not significantly associated with sexual size dimorphism or limitation of ornaments. Although mode of locomotion and predictability of food were hypothesized to restrict the expression of secondary sexual characters in females more than in males, this was clearly not the case. It is therefore unlikely that any of these

variables influenced the associations between sex limitation of ornaments and either mating system or male parental care. Sexual size dimorphism and sex-limited expression of secondary sexual characters were significantly associated with the social mating system and male parental behavior, but not with migration, diet and foraging mode. This observation suggests that selection pressures during reproduction rather than during the nonreproductive season affect the evolution of sexual size dimorphism of ornaments. This suggestion is also consistent with previous studies of sexual size dimorphism and dichromatism in birds (Martin and Badyaev, 1996; Promislow et al., 1992, 1994).

We have found no significant relationship between sexual size dimorphism of ornaments and the ecological variables, and only slightly less sexual size dimorphism of ornaments in species in which males fed the young as compared to those in which they did not feed. This lack of relationship between dimorphism and the ecological factors could be due to absence of effect on either sex, but also due to an equal effect of the ecological factors on both sexes. Our analyses suggest that the former is the most plausible explanation because we have found no significant relationship between the ecological

variables and relative size of ornaments for each sex separately. However, these results should be also considered with caution because they are based on a small number of standardized linear contrasts, and the power of the tests is hence moderate to low (power analyses; in all 18 tests: power ≤ 0.47 , $d \leq 0.82$, $\alpha = 0.05$, $5 \leq n \leq 14$).

In conclusion, relatively large male (but not female) secondary sexual characters, high degrees of polygyny, and absence of male parental care are significantly associated with sex limitation of ornament expression in bird species with extravagant feather ornaments.

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APPENDIX
Type of feather ornament, length of morphological characters (SE), and ecological variables in bird species included in this study

Species and ornament	Sex	n	Wing length (mm)	Ornament length (mm)	Mating system	Male nest building	Male incubation	Male feeding	Food	Foraging mode	Migration	References ^a
<i>Agelaius phoeniceus</i> , outer tail feathers (M, F)	M	10	70.25 (0.44)	127.95 (3.64)	Polygynous	Yes	No	No	Vegetable	Aerial	Resident	22,32,60
	F	10	58.00 (0.59)	41.25 (1.07)								
<i>Amblyornis subalaris</i> , crest (M)	M	10	122.25 (0.74)	37.50 (0.82)	Lekking	No	No	No	Fruit	Perching	Resident	2,11,15,26
	F	10	122.75 (1.19)	—								
<i>Anaethetus regillioides</i> , crest (M, F)	M	8	52.06 (0.63)	17.88 (0.85)	Monogamous	Yes	No	Yes	Animal	Perching	Resident	22,44,57
	F	7	49.93 (0.56)	15.86 (0.81)								
<i>Anas falcata</i> , wing feathers (M, F)	M	10	250.20 (1.63)	182.45 (3.28)	Monogamous	No	No	No	Vegetable	Swimming	Migratory	7,14,19,35,37
	F	10	231.05 (1.23)	100.70 (3.50)								
<i>Anas platyrhynchos</i> , central tail feathers (M)	M	10	269.00 (4.19)	64.20 (2.38)	Monogamous	No	No	No	Vegetable	Swimming	Partial	12,17,36,37,54
	F	10	249.50 (2.84)	—								
<i>Anthochaera carunculata</i> , central tail feathers (M, F)	M	10	154.95 (1.92)	159.95 (3.85)	Monogamous	—	—	Yes	Animal	Perching	Resident	5,47,48,53
	F	10	144.95 (2.84)	147.00 (2.27)								
<i>Aplonis metallica</i> , central tail feathers (M, F)	M	10	110.60 (0.41)	99.00 (1.54)	Monogamous	—	—	—	Fruit	Perching	Partial	2,5,48
	F	10	106.15 (1.06)	94.05 (1.81)								
<i>Aythya fuligula</i> , crest (M, F)	M	10	203.25 (1.55)	62.30 (2.83)	Monogamous	No	No	No	Vegetable	Diving	Partial	12,14,35,37
	F	10	194.50 (1.34)	24.10 (2.76)								
<i>Cardinalis cardinalis</i> , crest (M, F)	M	10	95.48 (1.00)	30.30 (0.67)	Monogamous	No	No	Yes	Vegetable	Perching	Resident	4,17,34,57
	F	10	91.65 (0.76)	28.80 (0.60)								
<i>Chiroxiphia linearis</i> , central tail feathers (M, F)	M	10	71.15 (0.41)	141.75 (4.06)	Lekking	No	No	No	Fruit	Perching	Resident	34,43,56,65
	F	10	70.15 (0.60)	54.30 (1.93)								
<i>Copsychus malabaricus</i> , central tail feathers (M, F)	M	10	96.50 (0.85)	171.60 (6.23)	Monogamous	No	No	Yes	Animal	Ground	Resident	1,45,49
	F	10	92.00 (1.38)	134.00 (2.99)								
<i>Coracias abyssinicus</i> , outer tail feathers (M, F)	M	10	161.90 (0.88)	238.75 (5.73)	Monogamous	No	—	—	Animal	Perching	Partial	8,25,50
	F	10	159.60 (1.80)	226.85 (5.02)								
<i>Dicrurus paradisaicus</i> , outer tail feathers (M, F)	M	10	161.80 (2.06)	356.25 (15.82)	Monogamous	Yes	Yes	Yes	Animal	Aerial	Resident	1,45,49
	F	10	156.05 (1.86)	322.50 (9.08)								
<i>Dinopium javanense</i> , crest (M, F)	M	10	133.15 (2.10)	23.80 (0.42)	Monogamous	Yes	Yes	Yes	Animal	Perching	Resident	1,49,71
	F	10	129.65 (1.45)	21.60 (0.95)								
<i>Diphylloides magnificus</i> , neck tuft (M)	M	10	113.75 (0.85)	41.00 (1.00)	Lekking	No	No	No	Fruit	Perching	Resident	2,3,11,15,26
	F	10	107.70 (0.54)	—								
<i>Dryocopus sabini</i> , upper tail coverts (M, F)	M	10	84.40 (0.98)	34.20 (0.49)	—	—	—	—	—	—	—	—
	F	10	80.60 (0.73)	32.00 (0.70)								
<i>Eremophila alpestris</i> , head plumes (M, F)	M	10	109.40 (0.73)	9.53 (0.20)	Monogamous	No	No	Yes	Vegetable	Ground	Partial	1,12,14,17,19
	F	10	102.45 (1.14)	7.69 (0.25)								
<i>Erythrura prasina</i> , central tail feathers (M, F)	M	10	58.73 (0.22)	59.63 (1.38)	Monogamous	Yes	Yes	Yes	Vegetable	Ground	Resident	9,28,49
	F	10	59.53 (0.31)	41.38 (1.14)								
<i>Euplectes jacksoni</i> , central tail feathers (M)	M	10	92.10 (0.76)	208.40 (2.11)	Lekking	No	No	No	Vegetable	Ground	Resident	43,50,70
	F	10	84.10 (0.69)	—								
<i>Gallus gallus</i> , neck feathers (M, F)	M	10	232.30 (3.24)	105.30 (3.66)	Polygynous	No	No	No	Vegetable	Ground	Resident	1,13,35,40,49
	F	10	198.50 (1.84)	54.35 (1.41)								
<i>Hirundo rustica</i> , outer tail feathers (M, F)	M	10	127.50 (1.29)	111.85 (2.27)	Monogamous	Yes	No	Yes	Animal	Aerial	Migratory	4,12,14,17,67
	F	10	125.90 (0.89)	91.55 (2.26)								
<i>Hirundo semirufa</i> , outer tail feathers (M, F)	M	10	118.25 (1.21)	114.50 (4.24)	Monogamous	Yes	No	—	Animal	Aerial	Partial	8,27,50,51,67
	F	10	117.15 (1.11)	102.15 (2.93)								

APPENDIX, Continued

Species and ornament	Sex	n	Wing length (mm)	Ornament length (mm)	Mating system	Male nest building	Male incubation	Male feeding	Food	Foraging mode	Migration	References ^a
<i>Hydrophasianus chinurgus</i> , central tail feathers (M, F)	M	10	197.35 (4.61)	240.30 (13.31)	Polyandrous	Yes ^b	No ^b	No ^b	Animal	Ground	Partial	1,7,19,31,52
<i>Lophortyx californica</i> , head plumes (M, F)	F	10	221.55 (4.50)	287.65 (13.25)	Monogamous	No	No	Yes	Vegetable	Ground	Resident	4,17,34,35,41
<i>Macrodipteryx longipennis</i> , wing feathers (M)	M	10	113.78 (0.89)	32.70 (0.72)	Polygynous	No	No	—	Animal	Aerial	Migratory	8,50,70
<i>Macrodipteryx longipennis</i> , wing feathers (M)	F	10	179.45 (1.28)	450.30 (12.17)	Monogamous	No	No	Yes	Animal	Ground	Resident	5,48,61
<i>Madurus splendens</i> , moustache (M)	M	10	168.55 (0.97)	—	Monogamous	Yes	No	Yes	Vegetable	Ground	Partial	1,19,58
<i>Madopus lathami</i> , crest (M, F)	M	10	84.70 (0.51)	24.50 (0.48)	Lekking	No	No	No	Animal	Ground	Resident	5,43,48,55,63
<i>Menura superba</i> , central tail feathers (M, F)	F	8	272.19 (6.38)	612.45 (23.56)	Monogamous	Yes	No	Yes	Vegetable	Perching	Resident	20,50,70
<i>Nectarinia johnstoni</i> , central tail feathers (M)	M	10	79.45 (1.13)	482.81 (9.86)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	1,19,49
<i>Orthotomus sutorius</i> , central tail feathers (M, F)	M	10	71.55 (1.20)	155.70 (6.80)	Monogamous	Yes	No	No	Vegetable	Ground	Partial	12,14,19,42,43
<i>Otis tarda</i> , moustache (M, F)	M	10	50.03 (0.57)	78.05 (4.55)	Monogamous	Yes	No	Yes	Vegetable	Perching	Resident	12,14,19,23
<i>Panurus biarmicus</i> , moustache (M, F)	F	10	46.68 (0.49)	38.30 (1.00)	Lekking	No	No	No	Fruit	Perching	Resident	11,15,26,43
<i>Paradisaea rubra</i> , central tail feathers (M)	M	10	603.50 (7.66)	128.90 (6.31)	Monogamous	Yes	No	No	Vegetable	Ground	Resident	32,34,43,56,62
<i>Phaethornis superciliosus</i> , central tail feathers (M, F)	M	10	470.30 (4.62)	23.40 (2.27)	Monogamous	Yes	No	No	Fruit	Perching	Resident	4,17,34
<i>Phainopepla nitens</i> , crest (M, F)	M	10	60.00 (0.48)	12.05 (0.25)	Monogamous	Yes	No	Yes	Fruit	Perching	Resident	34,56,65,69
<i>Pharomachrus mocinno</i> , tail coverts (M, F)	F	10	58.15 (0.26)	9.40 (0.19)	Lekking	No	No	No	Animal	Ground	Migratory	12,14,23,31,43
<i>Philomachus pugnax</i> , neck tuft (M)	M	10	168.80 (1.00)	517.00 (4.84)	Lekking	No	No	No	Fruit	Perching	Resident	43,57,60,62
<i>Pipra cornuta</i> , crest (M)	F	—	152.60 (1.55)	—	Lekking	No	No	Yes	Vegetable	Aerial	Resident	30,57,60,62
<i>Pitohys albigrons</i> , crest (M, F)	M	10	59.55 (0.41)	72.10 (0.74)	Monogamous	Yes	No	Yes	Fruit	Perching	Partial	12,14,23,35,52
<i>Podiceps cristatus</i> , ear tuft feathers (M, F)	M	10	60.20 (1.02)	68.65 (1.01)	Monogamous	Yes	No	Yes	Fruit	Perching	Resident	21,59,66
<i>Prothemadura novaeseelandiae</i> , neck feathers (M, F)	M	10	93.75 (0.80)	25.50 (0.37)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	8,50,67
<i>Psittacula longicauda</i> , central tail feathers (M, F)	F	10	91.85 (1.36)	20.80 (0.49)	Lekking	No	No	—	Animal	Aerial	Resident	24,45,49
<i>Pteridophora alberti</i> , crown feathers (M, F)	M	9	210.30 (1.73)	752.45 (29.94)	Lekking	No	No	No	Vegetable	Perching	Resident	2,11,15,26,43
	F	10	186.10 (1.33)	39.45 (1.34)	Lekking	No	No	No	Fruit	Perching	Resident	
	M	10	153.10 (1.03)	15.40 (0.32)	Lekking	No	No	No	Fruit	Perching	Resident	
	F	—	66.55 (0.43)	—	Lekking	No	No	No	Fruit	Perching	Resident	
	M	10	72.55 (0.57)	20.80 (1.05)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	
	F	10	70.15 (0.65)	17.45 (0.68)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	
	M	10	188.50 (1.44)	39.95 (1.27)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	
	F	10	183.85 (1.73)	36.30 (1.32)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	
	M	10	151.95 (2.05)	33.45 (0.93)	Monogamous	No	No	Yes	Animal	Ground	Resident	
	F	10	140.85 (2.26)	30.65 (1.05)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	
	M	10	97.35 (0.76)	97.85 (3.51)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	
	F	9	88.28 (0.83)	68.67 (2.96)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	
	M	10	178.68 (0.90)	242.88 (3.30)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	
	F	10	169.25 (1.62)	180.40 (7.65)	Monogamous	Yes	No	Yes	Animal	Ground	Resident	
	M	9	123.89 (1.29)	435.11 (15.26)	Lekking	No	No	No	Vegetable	Perching	Resident	
	F	—	—	—	Lekking	No	No	No	Vegetable	Perching	Resident	

APPENDIX, Continued

Species and ornament	Sex	n	Wing length (mm)	Ornament length (mm)	Mating system	Male nest building	Male incubation	Male feeding	Food	Foraging mode	Migration	References ^a
<i>Pylogonys caudatus</i> , central tail feathers (M, F)	M	10	97.10 (0.61)	133.10 (2.77)	Monogamous	Yes	No	Yes	Fruit	Aerial	Resident	56,65,69
	F	7	94.71 (0.71)	116.07 (2.11)								
<i>Ptiloris magnificus</i> , flank plumes (M, F)	M	10	186.45 (0.96)	179.30 (4.42)	Lekking	No	No	No	Animal	Perching	Resident	3,11,15,26,43
	F	10	156.30 (1.86)	72.90 (2.13)								
<i>Quiscalus mexicanus</i> , central tail feathers (M, F)	M	10	199.45 (2.67)	199.60 (6.48)	Polygynous	No	No	No	Vegetable	Ground	Partial	4,17,32,34,57
	F	10	160.40 (2.07)	149.95 (4.62)								
<i>Rollulus rouloul</i> , crest (M, F)	M	10	140.30 (1.53)	37.50 (1.72)	Monogamous	—	No	No	Vegetable	Ground	Resident	35,41,49
	F	10	139.95 (0.92)	—								
<i>Rupicola peruviana</i> , crest (M, F)	M	10	191.25 (1.13)	30.45 (0.67)	Lekking	No	No	No	Fruit	Aerial	Resident	32,43,57,64
	F	10	181.40 (1.79)	20.05 (0.81)								
<i>Scotornis climacurus</i> , central tail feathers (M, F)	M	10	142.30 (1.21)	218.45 (7.58)	Monogamous	No	—	—	Animal	Aerial	Partial	8,50,70
	F	10	143.45 (1.42)	172.35 (5.10)								
<i>Sturnus unicolor</i> , throat feathers (M, F)	M	10	130.90 (0.45)	32.60 (1.22)	Monogamous	Yes	Yes	Yes	Vegetable	Ground	Resident	12,18,33
	F	10	127.20 (0.79)	22.70 (0.94)								
<i>Syrhaptes paradoxus</i> , central tail feathers (M, F)	M	10	237.65 (6.29)	167.90 (6.87)	Monogamous	—	Yes	No	Vegetable	Ground	Partial	12,14,19,23,42
	F	10	225.70 (2.28)	126.55 (3.30)								
<i>Tanyptera galatea</i> , central tail feathers (M, F)	M	10	108.60 (0.83)	242.55 (4.70)	Monogamous	Yes	—	Yes	Animal	Ground	Resident	2,10,25
	F	10	107.95 (1.53)	204.00 (10.20)								
<i>Terpsiphone viridis</i> , central tail feathers (M, F)	M	10	84.65 (1.13)	272.55 (13.20)	Monogamous	—	Yes	Yes	Animal	Aerial	Partial	27,50,51
	F	10	77.30 (0.72)	85.95 (3.08)								
<i>Tetrao tetrix</i> , outer tail feathers (M, F)	M	10	254.85 (1.55)	173.50 (3.87)	Lekking	No	No	No	Vegetable	Ground	Resident	12,14,35,39,46
	F	10	223.70 (2.79)	105.20 (2.51)								
<i>Theron apicauda</i> , central tail feathers (M, F)	M	10	172.05 (1.68)	181.50 (2.39)	Monogamous	—	Yes	Yes	Fruit	Perching	Resident	1,29,45
	F	10	167.90 (1.31)	150.55 (4.08)								
<i>Trochilus polytmus</i> , 2nd outer tail feathers (M, F)	M	10	66.60 (0.60)	169.50 (3.85)	Polygynous	No	No	No	Vegetable	Aerial	Resident	6,16,68
	F	10	57.44 (0.56)	39.75 (1.30)								
<i>Tyrannus savana</i> , outer tail feathers (M, F)	M	10	111.35 (1.39)	239.25 (10.46)	Monogamous	Yes	Yes	Yes	Animal	Aerial	Partial	32,34,57,62,69
	F	10	105.40 (0.92)	178.00 (7.33)								
<i>Vanellus vanellus</i> , crest (M, F)	M	10	224.60 (1.56)	78.45 (2.67)	Monogamous	Yes	Yes	No	Animal	Ground	Partial	12,14,23,31,38
	F	10	222.10 (2.14)	52.60 (3.79)								
<i>Vidua macroura</i> , central tail feathers (M)	M	10	73.40 (0.77)	215.45 (5.03)	Lekking	No	No	No	Vegetable	Ground	Resident	27,43,50,51
	F	10	69.68 (1.05)	—								

^a Sources of information concerning the ecological variables of the bird species considered in this study: 1. Ali S, Ripley SD, 1987. Compact handbook of the birds of India and Pakistan, 2nd ed. Delhi: Oxford University Press; 2. Beehler BM, Pratt TK, Zimmerman DA, 1986. Birds of New Guinea. Princeton, New Jersey: Princeton University Press; 3. Beehler B, Pruett-Jones S, 1983. Display dispersion and the diet of birds of paradise: a comparison of nine species. Behav Ecol Sociobiol 13:229-238; 4. Bent AC, et al., 1919-1968. Life histories of North American birds, 16 vols. US Natl Museum Bull; 5. Blakers M, Davies SJFF, Reilly PN, 1984. The atlas of Australian birds. Carlton: Melbourne University Press; 6. Bond J, 1974. Birds of the West Indies, 4th ed. London: Collins; 7. Brazil MA, 1991. The birds of Japan. London: Christopher Helm, A & C Black; 8. Brown LH, Urban EK, Newman K, Fry CH, Keith S (eds), 1982-1992. The birds of Africa, 4 vols. London: Academic Press; 9. Clement P, Harris A, Davis J, 1993. Finches & sparrows. An identification guide. London: Christopher Helm, A & C Black; 10. Coates BJ, 1985-1990. The birds of Papua New Guinea, including the Bismark Archipelago and Bougainville, 2 vols. Alderley: Dove Publications; 11. Cooper WT, Forshaw JM, 1977. The birds of paradise and bower birds. Sydney: Collins; 12. Cramp S, Simmons KEL, Perrins CM, eds, 1977-1994. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic, 9 vols. Oxford: Oxford University Press; 13. Delacour J, 1977. The pheasants of the world, 2nd ed. Surrey: Spur Publications; Suffolk: The World Pheasant Association; 14. Dement'ev GP, Gladkov NA, eds, 1966-1970. Birds of the Soviet Union, 6 vols. Jerusalem: Israel Program for Scientific Translations; 15. Diamond J, 1986. Biology of birds of paradise and bowerbirds. Annu Rev Ecol Syst 17:17-37; 16. Downer A, Sutton R, 1990. Birds of Jamaica. A photographic field guide. Cambridge: Cambridge University Press; 17. Ehrlich PR, Dobkin DS, Wheye D, 1988. The birder's handbook. A field guide to the natural history of North American birds. New York: Simon & Schuster; 18. Etchécopar RD, Hùe F, 1967. The birds of North Africa from the Canary Islands to the Red Sea. Edinburgh: Oliver & Boyd; 19. Etchécopar RD, Hùe F, 1978-1983. Les oiseaux de Chine, de Mongolie et de Corée, 2 vols. Papeete: Les

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^b Female parental care.

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