Ecology and evolution of extravagant feather ornaments

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Abstract

The ancestral conditions that permit the evolution of extravagant secondary sexual characters are of considerable theoretical and empirical interest because they allow identification of necessary ecological conditions, but also allow empirical tests of models of female mate preferences. We investigated the ancestral and derived state of a range of ecological and evolutionary variables that might have been implicated in the evolution of secondary sexual characters. Extravagant feather ornaments have evolved independently at least 70 times in birds, and the context of these evolutionary events was investigated statistically. The acquisition of feather ornaments was significantly associated with a change in social mating system from monogamy to polygyny or lekking. This association is consistent with the Fisherian mechanism of sexual selection. However, very often also the acquisition of feather ornaments occurred without change in mating system. Therefore, ornamentation can develop for reasons other than polygyny. We did not find any indication of male parental care, kind of food, foraging mode, coloniality, nest site, migration or body mass being significantly associated with a change in the state of ornamentation.

Introduction

Despite only a fraction of all organisms having evolved extravagant secondary sexual characters, these have played an important conceptual, theoretical and empirical role in evolutionary biology (Darwin, 1871; Cronin, 1991; Andersson, 1994). Secondary sexual characters such as the antlers of deer and the train of the blue peacock Pavo cristatus are presumed to have arisen and be maintained as a result of directional sexual selection. Individuals with more extreme character values are expected to benefit in terms of male-male competition and/or female choice, respectively. An evolutionary understanding of sexual selection not only requires knowledge of the maintenance, but also of the origin of the characters in question. Almost the entire current surge in interest of sexual selection has been focused on the maintenance of secondary sexual characters based on observational and

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experimental studies of male–male competition and female choice (Andersson, 1994; Møller, 1994). The origin of extravagant ornamentation is, however, equally interesting for a complete understanding of sexual selection. Andersson (1994) in his recent review of sexual selection listed only five comparative studies of sexual ornamentation (Clutton-Brock *et al.*, 1977, 1980; Höglund, 1989; Møller & Pomiankowski, 1993; Höglund & Sillén-Tullberg, 1994), and none of these addressed the question of the ecological conditions being associated with the evolution of extravagant ornamentation.

Models of sexual selection can be classified in different ways (Andersson, 1994; Møller, 1994), but here we adopt a classification based on the kinds of benefits acquired by individuals of the choosy sex, usually females. Fitness benefits obtained by choosy individuals are either direct or indirect. Direct fitness benefits can be obtained in terms of parental care, a high fertilizing ability, absence of contagious parasites, territory quality, nuptial gifts or other kinds of resources (reviews in Andersson, 1994; Møller, 1994). Indirect fitness benefits are either so-called good genes that enhance the viability of offspring (Zahavi, 1975, 1977; Hamilton & Zuk, 1982; Andersson, 1986; Heywood, 1989; Iwasa et al., 1991; Folstad & Karter, 1992) or arbitrary attractiveness genes that increase the mating success of sons (Fisher, 1930; Lande, 1981; Pomiankowski et al., 1991). These different kinds of models make certain assumptions or predictions concerning the conditions that are particularly likely to precede the evolution of extravagant secondary sexual characters. Models of direct fitness benefits assume that features of direct benefits provided by individuals of the chosen sex are likely to be present before and particularly after the evolution of the secondary sexual character. Models of viability indicators do not make any predictions concerning resources provided by males, although one might predict that costly activities would be more likely to render signals reliable quality-indicators. Models of pure attractiveness predict that secondary sexual characters would be particularly suitable as female attractants in socially polygynous and particularly in lekking mating systems, although the mechanism might work, albeit in a weaker form, in socially monogamous mating systems.

Currently, we have only got the slightest knowledge of the ecological conditions that are associated with a change in state of extravagant ornamentation. Here we report on a comparative study of the ecological conditions associated with the evolution of a particular kind of secondary sexual characters: extravagant feather ornaments in birds, that is to say, feathers elongated in an exaggerated way, mainly in one of the sexes (generally males), as those of a peacock's train, a pheasant's tail and various feather traits in birds of paradise. These characters have played an important role in our understanding of sexual selection from the initial writings of Charles Darwin (1871) to more recent experimental studies (e.g. Andersson, 1982; Møller, 1988, 1992; Jones & Hunter, 1993). There is ample observational and experimental evidence for extravagant feather ornaments being involved in female choice (Andersson, 1982, 1992; Møller, 1988, 1992, 1994; Barnard, 1990; Petrie et al., 1991; Smith et al., 1991; Evans & Hatchwell, 1992; Saino et al., 1997d), while the same studies provide no or very little evidence for an effect on male-male competition. Feather ornaments are therefore primarily considered to be involved in female choice throughout this paper. They represent a suitable category of secondary sexual characters for study because they are easy to identify, they have evolved independently a very large number of times, and the ecological variables of interest are relatively well known in birds in general. The phylogenetic relationships of birds are also relatively well known allowing for proper analyses of the character transitions.

Methods

Definition of feather ornaments

We have identified independent evolutionary events of feather ornamentation in all extant birds. Sexual size dimorphism was considered either with or without complete sex limitation. 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 & Hunter, 1993). 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 Introduction). Sexual size monomorphism was not the subject of the present study. Furthermore, we have not considered either feather colours 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 size of at least 5% because previous studies have considered this cut-off point for dimorphism (Höglund, 1989; Oakes, 1992; Höglund & Sillén-Tullberg, 1994). Species investigated were recorded from extensive searches of the literature and major European museum collections (see Acknowledgments). If we suspected that a species might be sexually size dimorphic in a feather character, we investigated this by measuring 10 males and 10 females of the species in question. A total of 82 such cases resulted in 12 being considered to be sexually size monomorphic, according to the criterion stated above, and the rest being sexually size dimorphic. A few bird species could not be included in our data set, or even classified as sexually size dimorphic or monomorphic, owing to a shortage of specimens in the museum collections visited. Although the list of sexually size dimorphic species is the largest so far, we cannot exclude the possibility that we have missed a few cases of slight sexual size dimorphism. The degree of dimorphism (((male size – female size)/(female size)) \times 100) among species included in the present study ranged from 5% to 450.9% in species with partial sex limitation of ornament expression, with a mean value of 68.4% (SE = 13.4, n = 49 species). Moreover, ornament dimorphism was not due to a general difference in body size between sexes, because in the 41 species with males having longer tarsus than females, ornament dimorphism (as defined above) was on average 33.9 times larger than tarsus dimorphism (SE = 8.0), and always more than 1.5 times larger. Species with a feather character only being expressed in males were all included in the study.

Phylogenetic information

We searched for phylogenetic information on the relationships between extant birds, but were forced to rely on taxonomic information in a number of cases. To this end we have used two different taxonomies: that of Sibley & Ahlquist (1990) based on DNA–DNA hybridization and that of Howard & Moore (1991) based on classical taxonomical information. Sibley and Ahlquist have been criticized for their methods (e.g. Krajewski, 1991; O'Hara, 1991; Raikow, 1991) and many recent phylogenies using sequence data differ from theirs (see Mindell, 1997). However, they have also been supported by other studies (Harshman, 1994; Mooers & Cotgreave, 1994; Sibley, 1994; Bleiweiss et al., 1995). Therefore, we assessed the reliability of the analyses based on Sibley and Ahlquist 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; Sheldon & Winkler, 1993; Bleiweiss et al., 1994). The supplementary 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 that were unsupported by the alternative phylogenies. Hence, by relying on Sibley & Ahlquist (1990) we have used a conservative estimate of the number of evolutionary events. Our method of choosing independent ornamentation events is likely to be conservative because the intrafamiliar phylogenetic relationships are unknown for many families with many ornamented species.

Feather ornamentation has evolved 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 considered to be independent evolutionary events. If more than one trait had become exaggerated in a family, we considered this to represent a number of independent evolutionary events equalling 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, since these traits were obviously developmentally and morphologically independent.

Ornamented species were picked with respect to abundance if more than one choice was possible with the more abundant species being preferred owing to more ecological information being available for abundant species. We do not believe that latitudinal bias has been introduced in our sample as a result of the method of choice, since tropical species are also very well represented in the European museums visited, especially in the British Museum (Natural History), Tring, UK, where most specimens were measured. Actually, 80% of the ornamented species included in this study have all or part of their breeding range within the tropics. For pairwise comparisons, we randomly chose a nonornamented species within the same genus, if possible, or otherwise within the same subfamily. Our pairs of species were not sister taxa in the normal sense of the word, since in many cases the nonornamented species was not necessarily the closest relative. However, this does not change the interpretation of the results.

Ecological variables

Mating system

Species were classified as (1) socially monogamous if a male and a female associated for reproduction, (2) polygynous if at least 5% of the males in one population was associated with more than a single female for reproduction, (3) polyandrous if at least 5% of the females was associated with more than a single male for reproduction and (4) lekking if males aggregated at communal display grounds where females arrived to make their mate choice.

Male parental care

Male expenditure of reproductive effort on nest building, incubation and offspring provisioning was determined. Too little information was available for courtship feeding to allow this variable to be included. Species were classified as having no or some male contribution for each of the three categories. A more fine-scaled classification was impossible owing to lack of quantitative information for many species.

Food

Specific kinds of food may render extravagant ornaments less costly, if superabundant and predictable, and thereby reduce the costs of ornamentation. Other kinds of food may be difficult to obtain and constrain the evolution of ornamentation. We classified species as frugivorous if they mainly ate fruit, and consumers of animal food if they subsisted on invertebrates or vertebrates. The rest of the species were lumped together in a single category.

Foraging mode

Birds differ in their foraging modes and a number of different classifications are possible. Since our emphasis was on the consequences of costly behaviour for the likelihood of evolution of extravagant ornaments, we attempted to obtain estimates of these modes while lumping the rest. Aerial foragers obtain all their food from pursuing food (usually invertebrates) in flight. Divers pursue food while diving.

Coloniality

Social organization was classified as either colonial or solitary depending on whether nests were closely aggregated or dispersed.

Nest site

Bird species were classified as hole nesters or open nesters depending on whether they used holes or open sites for their nests.

Migration

Bird species were classified as migrants, partial migrants or residents depending on whether there was no overlap, some overlap or complete overlap between breeding and nonbreeding ranges due to seasonal movements.

Body mass

This was the average body mass for males and females.

The entire data set is listed in the Appendix. Information concerning the ecological variables of the bird species considered in this study was obtained from an extensive survey of the literature and from correspondence with scientists. The sources of information will be supplied to the readers upon request.

Comparative and statistical methods

We have used in this study a comparative method that control for similarities among species due to common ancestry. The pairwise comparative method contrasts the state of ecological variables of interest in closely related species differing in their degree of feather ornamentation (Felsenstein, 1985; Birkhead et al., 1987; Møller & Birkhead, 1992). For simplicity and methodological rigour we have employed a pairwise comparative approach to our questions by making comparisons between species with feather ornaments and a closely related relative lacking feather ornaments. When the independent evolutionary events of extravagant feather ornamentation have been identified, pairwise statistical tests can be made with respect to the independent variable (for example, the social mating system). A common pattern of change is consistent with an evolutionary association between two variables of interest. The pairwise comparative method has the additional strength that potentially confounding variables will be controlled automatically because pairs of closely related species generally have a similar anatomy, physiology and ecology due to their common evolutionary past (Møller & Birkhead, 1992). These tests were usually performed using nonparametric statistics for paired comparisons (Wilcoxon matched-pairs signed-ranks test) because all variables investigated (except body mass) were nominal or ordinal.

Statistical tests were performed according to Sokal & Rohlf (1995) and Siegel & Castellan (1988). All tests are two-tailed and the level of significance 5%.

Results

Social mating system

High degrees of polygyny have since the days of Darwin been presumed to be associated with extravagant feather ornamentation (Darwin, 1871; Møller & Pomiankowski, 1993), although this assumption has not been generally supported by comparative analyses (Höglund, 1989; Höglund & Sillén-Tullberg, 1994).

We were able to identify the mating system for 65 pairwise comparisons. There was a change in mating

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system from a lower to a higher degree of mating skew being associated with acquisition of a feather ornament in 17 cases, while there were no changes in the opposite direction (Appendix; sign test, P < 0.001). This change was also significant in a pairwise comparison (Wilcoxon matched-pairs signed-ranks test, z = -3.74, P = 0.0002). Hence, the acquisition of extravagant feather ornamentation was indeed associated with a change in mating system from a lower to a higher degree of polygyny.

Male parental care

Male parental care has been invoked to be associated with the evolution of secondary sexual characters because males generally play a less important role in parental duties in species with more skewed mating success (Darwin, 1871; Orians, 1969). However, this prediction has never been tested.

Male parental care could only be classified as present or absent, and with this crude classification there was no evidence of a change in ornamentation being consistently associated with a change in male parental care. Most pairs of taxa showed no change at all in male care, and changes were not consistent among pairs with a change in the state of parental care (nest building: five pairs, two with an increase and three with a decrease; incubation: seven pairs, five with an increase and two with a decrease; offspring provisioning: six pairs, four with an increase and two with a decrease). These differences were not statistically significant (Wilcoxon matched-pairs signed-ranks tests, z < 1.13, P > 0.26).

Food and foraging mode

Various kinds of food and foraging modes have been presumed to be associated with mating system and sexual ornamentation (e.g. frugivory and lekking in birds of paradise (Beehler & Pruett-Jones, 1983)). However, we found no evidence for changes in character state of food or foraging mode being consistently associated with changes in ornamentation, although this conclusion was based on a small number of changes between sister taxa (Wilcoxon matched-pairs signed-ranks test; food: z = -0.83, NS; foraging mode: z = 0, NS).

Sociality

Coloniality has traditionally been assumed to be associated with a spatially and temporally unpredictable food source (Lack, 1968), and extravagant ornamentation would therefore be particularly costly in a species with a colonial lifestyle. Coloniality is widespread among birds and has arisen independently many times.

There were very few cases where the state of sociality had changed within pairs of taxa, and there was no consistent change in ornamentation associated with acquisition of a colonial state of life (ornamentation arose with a change from solitary to colonial breeding in four cases and with a change from colonial to solitary breeding in four cases, Wilcoxon matched-pairs signed-ranks test, z = 0, NS).

Nest site

Feather ornamentation was not significantly related to nest site when comparing sister taxa. Only three pairs showed a change in nest site during the transition from nonornamentation to ornamentation, and all were associated with a change from hole to open nesting (Wilcoxon matched-pairs signed-ranks test, z = 1.73, P = 0.08).

Migration

Migration is an energetically very costly activity that is widespread among birds. Extravagant ornamentation might therefore be predicted to be less likely to arise in association with costly migration because the costly activity would simply be prohibitive for the evolution of extravagant ornamentation.

There were relatively few cases of the state of migratory habits changing within pairs of taxa. The analysis showed no significant differences, with ornamentation being associated with a change to a higher level of migration in 11 cases and to a lower level of migration in six cases (Wilcoxon matched-pairs signed-ranks test, z = -1.03, NS).

Body mass

Male mass was slightly larger in ornamented than in nonornamented taxa but the difference was not significant (mass of ornamented species (mean (SE)): 437 g (173), n = 68; mass of nonornamented species: 236 g (79), n = 62; paired *t*-test based on \log_{10} -transformed data, t = 1.56, d.f. = 59, P = 0.12).

There was even less evidence of a difference in female body mass between ornamented and nonornamented species (mass of ornamented species (mean (SE)): 312 g (92), n = 58; mass of nonornamented species: 203 g (55), n = 52; paired *t*-test based on \log_{10} -transformed data, t = 1.35, d.f. = 45, P = 0.19).

Discussion

The comparative analyses of the evolution of extravagant feather ornaments revealed that only the effect of mating system on ornamentation was significant. Extravagant feather ornaments were more likely to evolve in association with a change in the mating system from less to more skewed social mating success. This result is consistent with the initial observations of Darwin (1871) that secondary sexual characters appear to be more common and exaggerated in polygynous birds. There are a number of different explanations for this observation. First, the Fisherian mechanism of coevolving arbitrary male traits and female preferences is more important in mating systems with a greater skew in mating success (Fisher, 1930; Lande, 1981; Pomiankowski et al., 1991). Second, polygynous and particularly lekking bird species generally provide less male parental care than males of monogamous species (Lack, 1968), and the reduced role of males in reproduction allows a larger fraction of reproductive resources being allocated to mating effort and ornamentation. The reduced importance of male parental care also renders extravagant ornamentation energetically less costly, and a larger proportion of resources can therefore be allocated to ornamentation. Our results, however, did not demonstrate any significant relationship between decrease of male parental care and feather ornamentation.

Despite the key finding of ornamentation being associated with a change towards polygyny or lekking, it is important to emphasize that in 48 out of 65 cases, no change in mating system occurred with a change in ornamentation. This result can be interpreted in two ways. First, skew in male mating success can be extreme even in socially monogamous species because extra-pair paternity can result in a considerable increase in the variance in male mating success (Kirkpatrick et al., 1990; Møller, 1998). A change in the variance in male mating success within a monogamous clade may therefore result in the evolution of extravagant ornamentation. Second, while particular ecological conditions may interfere with the evolution of extravagant ornamentation, this does not necessarily imply that such an evolutionary change will not happen. For example, while a particular mating system may not be associated with the acquisition of ornaments, other ecological conditions may permit the evolution of ornamentation.

Ornaments are particularly costly to produce and maintain if they comprise feathers. Feathers consist of costly biochemicals and their mere presence imposes flight costs on their bearers. There is currently considerable observational and experimental evidence for the costs of feather ornamentation among birds. For example, current ornamentation is traded against future ornamentation (Møller, 1989), males incur a survival cost from their ornamentation (Møller & de Lope, 1994; Saino et al., 1997a), ornamental feathers result in a foraging cost (Møller, 1989; Evans & Thomas, 1992; Møller et al., 1995), ornamental feathers give rise to a predation cost (Møller & Nielsen, 1997), and their presence gives rise to physiological costs (Saino et al., 1997b, c) and impaired immune function (Saino & Møller, 1996).

Two scenarios are possible for the link between the costs of ornamentation and ornament evolution. First, ornaments are predicted to evolve in ecological contexts where there are permissible amounts of energy available for ornament production and maintenance. Therefore,

they are only predicted to evolve in contexts where there is a change in state from more to less costly activities such as from a higher to a lower state of male parental care, from a more to a less costly mode of foraging, or from a less to a more predictable food source. Second, they are particularly likely to evolve in contexts where they reveal the phenotypic quality of their bearers from the very beginning (Fisher, 1930; Zahavi, 1975; Møller, 1994). Such a situation will provide choosy females with a considerable initial mating advantage because the ornament reliably reveals male quality, and the mate preference for more extremely ornamented males will therefore rapidly increase in frequency. These two not necessarily mutually exclusive ideas can be investigated using the ecological context of extravagant feather ornamentation. However, we found no indication for ornaments being more or less likely to evolve with a particular change in the cost of male activities.

Several previous studies have shown that changes in female traits, instead of changes in male traits, could be the origin of sexual dimorphism (dichromatism) in birds (Björklund, 1991; Irwin, 1994; Martin & Badyaev, 1996; Burns, 1998). These changes in female coloration have been interpreted as responses to social selection or nest predation. Although some of the variables included in our studies were specifically male orientated (e.g. male parental care), some others could be affecting males and females in a similar way (e.g. food, coloniality, migration) or even affect females to a larger extent (e.g. nest site). However, we found no significant relationship between these variables and the presence of sexual dimorphism. Only mating system was significantly related to sexual size dimorphism of ornaments, which seems to emphasize the importance of sexual selection on the evolution of ornamentation. However, the relationship between mating system and sexual dimorphism is not as clear-cut, since some studies have found a significant relationship between the two variables (Scott & Clutton-Brock, 1989; Oakes, 1992; Møller & Birkhead, 1994), while others have not (Møller, 1986; Höglund, 1989; Höglund & Sillén-Tullberg, 1994).

Sexual monomorphism may have been the ancestral state in birds (Temrin & Sillén-Tullberg, 1994). The evolutionary transition from absence to presence of extravagant feather ornaments was often associated with a change in social mating system from monogamy to polygyny or lekking, but very often this transition occurred without change in mating system. Thus, ornamentation can develop for reasons other than polygyny.

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Appendix

Social mating system and ecological variables in pairs of bird species in which an extravagant feather ornament has evolved.

Species	Mating system	Male nest building	Male incubation	Male food provisioning	Food	Foraging mode	Sociality	Nest site	Migration	Male mass (g)	Female mass (g)
Podiceps cristatus	monogamous	yes	yes	yes	animal	diving	colonial	open	partial	738	609
Podiceps dominicus	monogamous	yes	yes	yes	animal	diving	colonial	open	resident	129	116
Anas falcata	monogamous	no	no	no	vegetable	swimming	solitary	open	migratory	713	585
Anas strepera		no	no	no	vegetable	swimming	solitary	open	partial	990	849
Anas platyrhynchos	monogamous	no	no	no	vegetable	swimming	solitary	open	partial	1170.7	1042.8
Anas rubripes	monogamous	no	no	no	vegetable	swimming	solitary	open	partial	1400	1100
Aythya fuligula	monogamous	no	no	no	vegetable	diving	solitary	open	partial	763.9	710.9
Aythya marila		no	no	no	vegetable	diving	solitary	open	migratory	932	957
Clangula hyemalis	monogamous	no	no	no	animal	diving	solitary	open	migratory	932	814
Melanitta nigra	monogamous	no	no	no	animal	diving	solitary	open	migratory	1100	800
Tetrao tetrix	lekking	no	no	no	vegetable	walking	solitary	open	resident	1255	910
Lagopus leucurus	monogamous	no	no	no	vegetable	walking	solitary	open	resident	601	516
Lophortyx californica	monogamous	no	no	yes	vegetable	walking	solitary	open	resident	176	170
Colinus virginianus	monogamous	yes	yes	yes	vegetable	walking	solitary	open	resident	173	170
Rollulus rouloul	monogamous	–	no	no	vegetable	walking	solitary	open	resident	232	202
Ptilopachus petrosus	monogamous	no	no	no	vegetable	walking	solitary	open	resident	190	-
Gallus gallus	polygynous	no	no	no	vegetable	walking	solitary	open	resident	877	556.3
Bambusicola fytchii	monogamous	-	no	no	vegetable	walking	solitary	open	resident	319	278
Phasianus colchicus	polygynous	no	no	no	vegetable	walking	solitary	open	resident	1317	953
Lophura inornata	–	-	no	no	–	walking	–	open	resident	-	-
Pavo cristatus	lekking	no	no	no	vegetable	perching perching	solitary	open	resident	5000	3375
Galloperdix spadicea	monogamous	-	no	no	vegetable		solitary	open	resident	307.1	326
Otis tarda	lekking	no	no	no	vegetable	walking	solitary	open	partial	10640	3962.3
Neotis ludwigi	polygynous	no	no	no	vegetable	walking	solitary	open	resident	4525	2350
Hydrophasianus chirurgus	polyandrous	yes*	no*	no*	animal	walking	solitary	open	partial	126	231
Metopidius indicus	polyandrous	yes*	no*	no*	animal	walking	solitary	open	resident	165.4	297.7
Vanellus vanellus	monogamous	yes	yes	no	animal	walking	solitary	open	partial	211	226
Vanellus lugubris	monogamous	no	–	no	animal	walking	solitary	open	partial	109.5	113
Philomachus pugnax	lekking	no	no	no	animal	walking	solitary	open	migratory	171	104
Tryngites subruficollis	lekking	no	no	no	animal	walking	solitary	open	migratory	71	53
Syrrhaptes paradoxus	monogamous	–	yes	no	vegetable	walking	colonial	open	partial	268.2	239.3
Pterocles orientalis	monogamous	yes	yes	no	vegetable	walking	solitary	open	partial	428	383

Treron apicauda Treron fulvicollis	monogamous monogamous	- yes	yes -	yes -	fruit fruit	perching perching	1 1	open	resident resident	220 165.4	200 167.7
Psittacula Iongicauda Loriculus vernalis	monogamous monogamous	- yes	yes yes	- yes	vegetable vegetable	perching perching	colonial -	hole hole	resident resident	198.5 28.4	170.1 31.8
Scotornis climacurus Phalaenoptilus nuttallii	monogamous monogamous	0 0	- yes	yes	animal animal	aerial aerial	solitary solitary	open	partial partial	39.3 47.2	- 49.5
Macrodipteryx longipennis Nyctiphrynus ocellatus	polygynous monogamous	0 0	no yes	- yes	animal animal	aerial aerial	solitary solitary	open	migratory resident	40.7 42.4	48.5
Hydropsalis brasiliana Caprimulgus carolinensis	monogamous monogamous	0 0	yes no	yes no	animal animal	aerial aerial	solitary solitary	open	partial migratory	57 120	58.5 -
Phaethomis superciliosus Threnetes leucurus	lekking monogamous	0 0	o u	ou	vegetable animal	aerial aerial	solitary solitary	open	resident resident	5.3 5.6	6 5.1
Lophornis ornata Chlorestes notatus	polygynous polygynous	0 0	o u	оп	vegetable vegetable	aerial aerial	solitary solitary	open	resident resident	2.4 3.8	2.4 3.4
Trochilus polytmus Polytmus guainumbi	polygynous	0 0	o u	ou	vegetable vegetable	aerial aerial	solitary solitary	open	resident resident	5.2 5.4	4.8 4.7
Topaza pella Urochroa bougueri	lekking polygynous	0 0	o u	ou ou	vegetable vegetable	aerial aerial	solitary solitary	open	1 1	12.7 8.7	1 1
Oxypogon guerinii Opisthoprora euryptera	polygynous polygynous	2 2	on on	ou ou	vegetable vegetable	perching aerial	solitary solitary	open	resident resident	4.8	1 1
Aglaiocercus kingi Schistes geoffroyi	polygynous polygynous	yes no	o u	ou ou	vegetable vegetable	aerial aerial	solitary solitary	open	resident resident	4.8	1 1
Pharomachrus moccino Temnotrogon roseigaster	monogamous monogamous	yes yes	yes -	yes -	fruit fruit	perching -	solitary -	hole hole	resident reisdent	206 -	1 1
Tanysiptera galatea Actenoides monacha	monogamous monogamous	yes -	1 1	yes -	animal animal	walking walking	solitary solitary	hole hole	resident resident	61.5 -	- 62
Coracias abyssinicus Coracias naevia	monogamous monogamous	0 0	1 1	- yes	animal animal	perching perching	solitary solitary	hole hole	partial partial	91.4 168	92.3 168
Dinopium javanense Picus canus	monogamous monogamous	yes yes	yes	yes yes	animal animal	perching walking	solitary solitary	hole hole	resident resident	104.2 129	99.2 130.5
Pithys albifrons Gymnopithys rufigula	monogamous monogamous	yes	yes	yes yes	animal animal	perching -	1 1	open -	resident resident	20.7 29.4	20.4 28.4
Rupicola peruviana Lipaugus unirufus	lekking Iekking	0 0	on on	ou	fruit fruit	aerial perching	solitary solitary	open	resident resident	266 83.7	221 74.7

Appendix (Continued)

Species	Mating system	Male nest building	Male incubation	Male food provisioning	Food	Foraging mode	Sociality	Nest site	Migration	Male mass (g)	Female mass (g)
Pipra cornuta	lekking	no	no	no	fruit	perching perching	solitary	open	resident	-	-
Pipra erythrocephala	lekking	no	no	no	fruit		solitary	open	resident	12	13.3
Chiroxiphia linearis	lekking	no	no	no	fruit	perching	solitary	open	resident	16.8	19.1
Corapipo leucorrhoa	lekking	no	no	no	fruit	perching	solitary	open	resident	10.9	13.9
Tyrannus savana	monogamous	yes	yes	yes	animal	aerial	solitary	open	partial	32.8	29.8
Tyrannus tyrannus	monogamous	yes	no	yes	animal	aerial	solitary	open	migratory	42.7	-
Anairetes reguloides	monogamous	yes	no	yes	animal	perching	solitary	open	resident	5.9	-
Inezia subflava	monogamous	yes	no	yes	animal	perching	solitary	open	resident	8.8	8.5
Menura novaehollandiae	lekking	no	no	no	animal	walking	solitary	open	resident	1500	900
Atrichornis rufescens	monogamous	no	yes	yes	animal	walking	solitary	open	resident	-	
Eremophila alpestris	monogamous	no	no	yes	vegetable	walking	solitary	open	partial	31.9	30.8
Eremopterix australis	monogamous	no	yes	yes	vegetable	walking	solitary	open	resident	14	15
Hirundo semirufa	monogamous	yes	no	-	animal	aerial	solitary	open	partial	25.5	21.3
Hirundo preussi	monogamous	yes	-		animal	aerial	colonial	hole	partial	12.2	14
Hirundo rustica	monogamous	yes	no	yes	animal	aerial	colonial	open	migratory	18.7	18.5
Hirundo rufigula	monogamous	-	yes	yes	animal	aerial	colonial	hole	partial	-	-
Psalidoprocne obscura Psalidoprocne nitens	monogamous monogamous	yes yes	-	-	animal animal	aerial aerial	colonial solitary	hole hole	partial resident	9.4 9.5	10 10
Dryoscopus sabini	–	–	–	-	-	–	–	–	–	39.9	36.9
Tchagra minuta	monogamous	yes	yes		animal	perching	solitary	open	partial	33	34.7
Ptilogonys caudatus	monogamous	yes	no	yes	fruit	aerial	solitary	open	resident	39.1	33.5
Hypocolius ampelinus	monogamous	yes	yes	yes	fruit	aerial	colonial	open	migratory	54	52.8
Phainopepla nitens Phainoptila melanoxantha	monogamous monogamous	yes –	yes -	yes –	fruit fruit	perching perching	solitary solitary	open open	partial resident	24 56	-
Copsychus malabaricus	monogamous	no	no	yes	animal	walking	solitary	hole	resident	32	31
Copsychus saularis	monogamous	no	no	yes	animal	walking	solitary	hole	resident	37.9	34.5
Panurus biarmicus	monogamous	yes	yes	yes	vegetable	perching	colonial	open	resident	15.6	14.9
Paradoxornis gularis	–	–	-	-	vegetable	perching	-	open	resident	29	29
Orthotomus sutorius	monogamous	yes	yes	yes	animal	perching	solitary	open	resident	8.7	7.8
Orthotomus atrogularis	monogamous	–	yes	–	animal	perching	solitary	open	resident	8.1	7.3
Malurus splendens	monogamous	no	no	yes	animal	walking	solitary	open	resident	9.5	8.5
Malurus coronatus	monogamous	no	no	yes	animal	walking	solitary	open	resident	10.5	10
Terpsiphone viridis	monogamous	–	yes	yes	animal	aerial	solitary	open	resident	15.1	14.6
Chasiempis sandwichensis	monogamous	Ves	ves	ves	animal	aerial	solitary	open	resident	14	_

Nectarinia johnstoni Nectarinia notata	monogamous -	оці	о С і	yes -	vegetable vegetable	perching perching	solitary solitary	open	resident resident	5.1 14.5	- 20
Anthochaera carunculata Acanthagenys rufogularis	monogamous monogamous	1 1	I C	yes yes	animal animal	perching perching	solitary solitary	open	resident resident	125 47	- 11
Prosthemadera novaesselandiae	monogamous	ou	оц	yes	fruit	perching	solitary	open	resident	125	89.6
Manorina melanophrys	monogamous	ОИ	ОП	yes	animal	perching	colonial	open	resident	28.5	I
Melophus lathami Emberiza calandra	monogamous monogamous	yes no	0 0	yes no	vegetable vegetable	walking walking	solitary solitary	open	partial partial	23.7 51.3	21 42.2
Cardinalis cardinalis Caryothraustes canadensis	monogamous monogamous	OL I	0 0	yes yes	vegetable vegetable	perching perching	solitary -	open	resident resident	45.4 32.4	43.9 34.2
Quiscalus mexicanus Euphagus carolinus	polygynous monogamous	0 00	0 0	no yes	vegetable animal	walking walking	colonial colonial	open	partial migratory	191 64.3	107 55.2
Erythrura prasina Erythrura hyperythra	monogamous monogamous	yes yes	yes	yes yes	vegetable vegetable	walking walking	1 1	open -	resident resident	17.2 15.2	14.9 12.4
Vidua macroura Vidua funerea	lekking polygynous	0 0	0 0	on on	vegetable vegetable	walking walking	1 1	1 1	resident resident	17.2 15.2	14.9 12.4
Euplectes jacksoni Euplectes hordacea	lekking polygynous	no yes	0 0	оп	vegetable vegetable	walking walking	solitary colonial	open	resident resident	- 20.4	- 18.4
Aplonis metallica Aplonis cantoroides	monogamous monogamous	1 1	1 1	1 1	fruit fruit	perching perching	colonial solitary	open hole	partial resident	61 55	1 1
Sturrus unicolor Sturrus cineraceus	monogamous monogamous	yes yes	yes	yes yes	vegetable animal	walking walking	colonial colonial	hole hole	resident partial	93	87.4 -
Dicrurus paradisaeus Dicrurus ludwigii	monogamous monogamous	yes yes	yes I	yes -	animal animal	aerial aerial	solitary solitary	open	resident resident	70.5 26.7	71.5 -
Amblyornis subalaris Amblyornis inornatus	lekking Iekking	on on	0 0	on on	fruit fruit	perching perching	solitary solitary	open	resident resident	103 125	114
Pteridophora alberti Manucodia jobiensis	lekking monogamous	OL I	0 0	no yes	fruit fruit	perching perching	solitary solitary	open	resident resident	87 228	77 180
Ptiloris magnificus Manucodia ater	lekking monogamous	OL I	0 00	no yes	animal fruit	perching perching	solitary solitary	open	resident resident	194 238	128 208
Semioptera wallacei Paradigalla brevicauda	lekking polygynous	on on	0 0	on On	fruit fruit	perching perching	– solitary	- open	resident resident	163 173	135 163

Appendix (Continued)

Species	Mating system	Male nest building	Male incubation	Male food provisioning	Food	Foraging mode	Sociality	Nest site	Migration	Male mass (g)	Female mass (g)
Lophorina superba	lekking	no	no	no	fruit	perching perching	–	open	resident	87	67
Macgregoria pulchra	monogamous	no	no	yes	fruit		solitary	open	resident	279	206
Parotia lawesii	lekking	no	no	no	fruit	perching perching	solitary	open	resident	167	144
Loboparadisea sericea	–	-	-	-	fruit		–	open	resident	64	73
Diphyllodes magnificus	lekking	no	no	no	fruit	perching	solitary	open	resident	97	82
Loria Ioriae	polygynous	no	no	no	fruit	perching	–	open	resident	85	81
Paradisaea rubra	lekking	no	no	no	fruit	perching perching	solitary	open	resident	201	158
Lycocorax pyrrhopterus	monogamous	-	-	-	fruit		–	open	resident	302	266

The first species listed for each pair is the ornamented species and the second is the nonornamented species. For detailed explanation or variables, see Methods. The sources of information concerning the ecological variables will be provided to the readers upon request. *Female parental care.