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Social foraging and the evolution of white plumage

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ABSTRACT

The significance of social foraging to the evolution of avian plumage traits has received little attention. White plumage could increase conspicuousness against a dark background and serve as a passive recruitment signal to attract distant foraging companions. White plumage could thus be selected if white individuals obtain net fitness benefits by attracting conspecifics to feeding flocks. Species that benefit little from the presence of foraging companions should have a darker, more cryptic coloration to avoid attracting potential competitors. Flash marks – white patches on wings or tails, often hidden until individuals take flight – could also be more common in social species if such marks serve to increase flock cohesion. In a data set including pairs of closely related species with contrasting foraging sociality, social species possessed overall whiter plumage than non-social species but did not exhibit a higher frequency of flash marks. Several traits, such as habitat type, plumage dichromatism, male body mass, sexual size dimorphism, prey type, level of prey activity and social mating system, which could all influence plumage characteristics on their own, were not related to social foraging or to the expression of plumage traits. This study provides empirical support across a wide range of species for a relationship between social foraging and white plumage coloration in birds.

Keywords: birds, flash marks, pairwise comparative method, social foraging, white plumage.

INTRODUCTION

Birds show enormous variation both within and among species in the physical properties and coloration characteristics of their plumage (Baker and Parker, 1979; Butcher and Rohwer, 1989; Savalli, 1995). It is generally thought that plumage traits have evolved through the action of sexual or natural selection. Sexual selection can occur if more colourful or extravagantly ornamented individuals gain greater reproductive success (Ryan, 1997). Alternatively, plumage traits can provide survival advantages, for instance through predator avoidance by mimicry with the background or through warning coloration (Slagsvold *et al.*, 1995; Götmark, 1997). In general, plumage traits may be influenced by properties of the habitat where signals are produced and by the sensory capabilities of intended receivers such as mates or predators (Savalli, 1995).

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Certain plumage characteristics have been thought to enhance foraging efficiency and thus provide additional survival advantages. For instance, overall white coloration could increase conspicuousness against a dark background and operate as a passive recruitment signal that enables individual birds to locate distant foraging companions more efficiently, facilitating the formation of feeding flocks (Armstrong, 1971; Kushlan, 1977). In flocks, individuals can then benefit from an increased food intake rate or decreased anti-predator vigilance (Elgar, 1989; Beauchamp, 1998). In support of the hypothesis, heron (*Ardea* sp.) models painted white attracted more conspecifics than darker models (Kushlan, 1977; Caldwell, 1981). These results suggest that, if white individuals obtain overall fitness benefits by attracting conspecifics, this will lead to directional selection towards whiter plumage. A possible corollary is that species that benefit little from the presence of foraging companions should have a darker, more cryptic coloration to avoid attracting potential competitors.

Social foraging could also influence the evolution of more specific plumage characteristics. Some distinct white patterns, referred to as flash marks, occur on wings or tails and usually remain hidden until individuals take flight. The display of flash marks in a group of fleeing birds can create confusion and render capture of one particular individual more difficult for a predator (Brooke, 1998). In addition, the display of flash marks may facilitate synchronous group departure and thus increase flock cohesion. In shore birds, flash marks occur more commonly in species foraging in flocks (Brooke, 1998), but it is not clear whether the evolution of flash marks in these species is associated with a greater risk of predation or a greater need to preserve flock cohesion.

We examined the generality of the association between white coloration and social foraging in a large set of species with different morphological and ecological features. We wished to determine the role of the evolutionary transition between solitary and social foraging in addition to other potential confounding factors, such as habitat type, prey detection abilities, predation risk and social mating system, which could also have an influence on plumage coloration. We contrasted two plumage characteristics, namely the overall proportion of white and the occurrence of flash marks, in a data set involving a large number of closely related pairs of species with contrasting foraging sociality. Pairwise comparisons provide a control for potentially confounding factors, since closely related species usually show similar morphological and ecological traits due to their common ancestry (Møller and Birkhead, 1992; Maddison, 2000). To reduce further the effect of confounding factors, we documented plumage characteristics during the non-reproductive season as a control for possible inter-sexual communication involving white coloration.

METHODS

Data collection

We collected data on flocking behaviour, plumage coloration and other morphological and ecological traits from several sources, including books on avian ecology and behaviour and ornithological journals (see Appendix). Morphological and ecological traits included male body mass, sexual size dimorphism, plumage dichromatism, habitat type, mating system, diet type and level of prey activity. The criterion for data selection was a detailed knowledge of foraging sociality during the non-reproductive season.

Species were classified into one of three categories of flocking behaviour based on published evidence of aggregations during foraging activities: (1) strictly solitary, birds forage singly; (2) occasionally social, aggregations of more than two individuals occur under peculiar circumstances but are rare and often involve small groups; and (3) strictly social, individuals always search for food or feed in flocks. For the purpose of the analysis, categories 1 and 2 were pooled to create a dichotomous variable.

We used recent phylogenetic information based on molecular or morphological traits to form closely related pairs of species with contrasting foraging sociality. Hence, the analysis focused on evolutionary transitions from solitary to social foraging. A lack of variance in social foraging within clades often limited the number of species pairs that could be used for comparison. One phylogenetic tree could yield several pairs as long as pairs failed to share common branches. When several species were available as sister taxa, we selected, if possible, species that occurred in the same geographical area. When phylogenetic information was unavailable, we formed pairs by selecting two species from the same genera with a preference for species occurring in the same geographical area. We selected pairs from as many families as possible to reduce the problem of sampling repeatedly in the same clades.

We used descriptions of plumage coloration and colour pictures from the above sources to obtain an estimate of the proportion of white in the plumage of each species included in the data set. For each sex separately, the same observer (G.B.) estimated visually the proportion of white present on the ventral and dorsal sides of adult birds in the non-reproductive season. Scores could take one of six values, ranging from 0 (total lack of white) to 5 (all white). Values for the ventral and dorsal sides were averaged and the resulting scores for each sex were also averaged for an overall species score. In addition, the presence of flash marks was also noted. We defined flash marks as conspicuous dorsal white stripes or patches on the wings, lower back, rump or tail (Brooke, 1998). Ventral white patterns were not considered as flash marks except in some species in which the tail is raised and constantly wiggled to reveal white under tail feathers. The amount of white contributed by flash marks was removed from the plumage scores to provide an estimate of white coloration independent of the occurrence of flash marks.

We recorded male body mass, if available, during the non-reproductive season to provide a uniform assessment of body mass across species. We assessed presence or absence of sexual size dimorphism from comparisons of differences in body dimensions between the sexes. We coded species for the presence or absence of plumage dichromatism based on a description of plumage differences between the sexes during the non-reproductive season. We distinguished between preferences for open or closed habitats for each species on the basis of the amount of tree cover. Closed habitats included forested areas, while open habitats included areas mostly devoid of tree cover such as savannas, lakes or coastal shores. Mixed habitats included a mixture of the above two categories. We classified species into one of four categories of social mating system: (1) monogamous, one male and one female associate for reproduction; (2) polygynous, most males in the population associate with more than one female; (3) polyandrous, most females in the population associate with more than one male; and (4) lekking, males aggregate at communal display sites where females select mating partners. Diet type was classified as mostly vegetarian (including foliage, fruits and seeds) or mostly carnivorous, with a mixed category overlapping the above two classes. Finally, we classified level of prey activity as either passive, when prey cannot actively evade a predator (e.g. carrion,

hibernating invertebrates, soil and mud invertebrates, plant matter), or active, when prey can locate a predator visually and initiate evasive manoeuvres (e.g. flying insects, birds, fish, cephalopods).

Phylogenetic analysis

We used the pairwise comparative method to control for possible similarities among closely related species due to a common ancestry (Møller and Birkhead, 1992; Maddison, 2000). The Wilcoxon signed ranks test was used to test the hypothesis of consistent changes across the set of species pairs in the states of morphological and ecological variables associated with the two degrees of sociality. For each test, we only included pairs where the analysis of morphological or ecological variables revealed different values for each pair member (Read and Nee, 1995). We used the sequential Bonferroni test procedure to determine which of the various tests made with the same data set remained significant (Rice, 1989). For clarity, we present the *P*-values of the tests before performing the Bonferroni and also describe whether the correction modified their significance. Two species exhibited two stable, adult colour morphs. In these cases, we selected for analysis the morphs that differed from those occurring in the sister species.

RESULTS

The search in the published literature provided a total of 80 pairs of species with contrasting foraging sociality distributed among 38 families (Appendix). The white plumage score did not vary among social and non-social species in 24 pairs. Among the remaining 56 pairs with contrasting values for white plumage score, the social species possessed a whiter plumage than the non-social species in 45 pairs (80%) [mean difference in plumage score (standard deviation) = 0.92 (1.52), $S = 518$, $P < 0.0001$, significant after Bonferroni].

Flash marks occurred in both social and non-social members of a pair in 15 pairs and did not occur at all in 38 pairs. Among the 27 pairs with contrasting values for the presence of flash marks, flash marks occurred in the social species but not in the non-social species in 19 pairs (70%, $S = 77$, $P = 0.03$, non-significant after Bonferroni). In the 16 pairs with contrasting values for habitat type, social species in 15 pairs showed a greater preference for open habitats than non-social counterparts ($S = 59.5$, $P = 0.0005$, significant after Bonferroni).

After Bonferroni corrections, no other traits analysed were found to be significantly associated with foraging sociality (male body mass: $S = 39$, $P = 0.82$, $n = 70$; social mating system: $S = 1.5$, $P = 1.0$, $n = 6$; prey type: $S = 18$, $P = 0.30$, $n = 15$; prey activity: $S = 40.5$, $P = 0.078$, $n = 18$; sexual size dimorphism: $S = 27.5$, $P = 0.057$, $n = 13$; plumage dichromatism: $S = 52.5$, $P = 0.04$, $n = 20$).

We tested whether preference for more open habitat types could have inflated the differences in plumage coloration in the 56 pairs with contrasting values for white plumage score. The mean difference (standard deviation) in plumage score in the subset of data including pairs where the social species preferred more open habitats [1.46 (1.61), $n = 10$] was not different from that in the subset including pairs living in the same habitat type [0.80 (1.49), $n = 46$; Wilcoxon Mann-Whitney test, $S = 344$, $P = 0.25$].

DISCUSSION

Our results indicate that, across a wide range of avian species, the evolutionary transition from solitary to social foraging is associated with the proportion of white plumage. Species foraging in flocks possessed an overall whiter coloration but did not exhibit flash marks in significantly higher frequencies than closely related, non-social species.

With respect to overall coloration, the results support the hypothesis that white plumage may serve as a passive recruitment signal to attract distant foragers (Armstrong, 1971; Kushlan, 1977). The white plumage of several species of herons has long been thought to act as a recruitment signal (Kushlan, 1977; Caldwell, 1981; Smith, 1995). Among petrels and albatrosses, more social species showed a larger proportion of white in the plumage (Bretagnolle, 1993). In herons or sea birds, species often share similar ecological features and it is conceivable that traits unrelated to foraging sociality, such as predation risk, habitat type and social mating system, accounted for the selection of a whiter plumage. Here, we controlled for ecological similarities among closely related species and found strong support for the purported advantage of white plumage to socially foraging species.

Alternative hypotheses for the evolution of white plumage appear unlikely to explain differences in plumage related to social foraging. A higher risk of predation may select for more cryptic plumage (Bretagnolle, 1993; Slagsvold *et al.*, 1995; Haskell, 1996; Rytkonen *et al.*, 1998). Social species and non-social counterparts, however, showed similar body masses, suggesting that predation risk, which is often thought to covary as a function of body mass (Bretagnolle, 1993; Thiollay and Jullien, 1998), cannot provide a full explanation of the results. More direct correlates of predation risk are required to assess the role of predation risk in the evolution of white coloration in social species. Overall white coloration may be selected in species with more skewed social mating systems, as conspicuous coloration could enhance male displays (Snow, 1982; Savalli, 1995). However, we did not detect significant differences between social species and non-social counterparts in social mating system, sexual size dimorphism or plumage dichromatism.

Closed habitats may favour the evolution of brighter plumage to increase conspicuousness to conspecifics (Marchetti, 1993). In our study, non-social species occurred more frequently in closed habitats, suggesting that increased conspicuousness, if present, may only be useful in non-foraging contexts such as territorial displays. In addition, differences in white coloration between pairs of species were not related to differences in habitat type. Finally, choice of more active prey may select for more cryptic plumage to reduce predator detection (Götmark, 1987). However, in our study, level of prey activity was not related to foraging sociality.

Not all pairs of species with contrasting foraging sociality showed differences in overall white coloration. In addition, a few non-social species exhibited whiter plumage than their social counterparts. Obviously, ecological factors other than foraging sociality will influence the evolution of white plumage in birds. Selective forces may include factors such as predation risk, which may force smaller, more vulnerable species to adopt a more cryptic plumage regardless of foraging sociality. In such cases, natural selection could favour the evolution of other types of recruitment signals, such as food calls (Elgar, 1986; Brown *et al.*, 1991), that are not based on plumage coloration. Such recruitment signals only increase predation risk during emission, in contrast to the continuous display of information provided by feather coloration.

Social foraging was only weakly associated with the expression of flash marks. Although flash marks have been documented to a greater extent in social shorebird species, it would appear that the association between flocking and flash marks may be tied to specific clades that forage in similar, open habitats (Brooke, 1998). In our study, flash marks occurred in several asocial species, suggesting a role for non-social factors. For instance, displays of flash marks have been shown to flush out prey in one bird species (Jablonski, 1999). Flash marks could also be used for territorial displays, especially in closed habitats that restrict communication range (Marchetti, 1993). Clearly, more information on the social foraging behaviour of bird species is required to clarify the nature of ecological and social factors that shaped the evolution of flash marks.

Functional analyses of plumage coloration have mostly focused on inter-sexual communication and interspecific signals to predators or prey. Here we have shown an association between plumage coloration and foraging sociality across a broad range of avian species. It remains to be determined whether social foraging selected for the evolution of white plumage traits or whether the presence of white plumage facilitated the evolution of social foraging.

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APPENDIX

Species[a]	Plumage score	Flash marks	Male body mass (g)	Size dimorphism	Dichromatic plumage	Mating system	Diet	Prey type	Habitat	References[b]
Social species whiter: flash marks present in social species only										
Sarkidiornis melanotos	1	yes	1 955	M > F	yes	polygyny	animal	mixed	open	18, 22, 26
Hymenolainus malacorhynchos	0	no	897	M > F	no	monogamy	animal	mixed	open	11, 22, 26
Hydrophasianus chirurgicus	2	yes	126	M < F	no	polyandry	mixed	passive	open	47, 48, 49
Jacana spinosa	0	no	104	M < F	no	polyandry	mixed	mixed	open	4, 47, 48, 49
Tringa glareola	1.5	yes	54	M < F	no	monogamy	animal	mixed	open	34, 47, 49, 50
Heteroscelus brevipes	0.5	no	117	M < F	no	monogamy	animal	passive	open	47, 49, 51
Larus argentatus	2.5	yes	977	M > F	no	monogamy	animal	mixed	open	50, 53
Stercorarius parasiticus	0	no	421	M < F	no	monogamy	animal	active	open	50, 53, 54
Haematopus ostralegus	2	yes	552	M = F	no	monogamy	animal	passive	open	47, 49, 50
Haematopus fuliginosus	0	no	740	M = F	no	monogamy	animal	passive	open	47, 49, 56
Himantopus himantopus	1	yes	164	M > F	no	monogamy	animal	mixed	open	47, 49, 50, 56
Himantopus novaezelandiae	0	no	157	M > F	no	monogamy	animal	mixed	open	47, 49, 56
Diomedea melanophrys	2.5	yes	3 710	M > F	no	monogamy	animal	active	open	11, 58, 59, 60
Phoebetria fusca	0	no	2 730	M > F	no	monogamy	animal	active	open	11, 58, 59, 60
Chrysolophus amherstiae	0.5	yes	763	M > F	yes	polygyny	mixed	passive	mixed	4, 42, 65
Chrysolophus pictus	0	no	692	M > F	yes	polygyny	mixed	passive	mixed	4, 42, 65
Columba livia	1	yes	369	M > F	yes	monogamy	vegetable	passive	open	67, 68
Columba bollii	0	no	500	M = F	no	monogamy	vegetable	passive	mixed	67, 68
Calyptorhychus latirostris	0.5	yes	653	M = F	yes	monogamy	vegetable	passive	closed	69, 80
Calyptorhychus lathamii	0	no	463	M > F	yes	monogamy	vegetable	passive	closed	69, 80
Hirundo pyrrhonata	1.5	yes	239	M = F	no	monogamy	animal	mixed	open	81, 82, 83
Hirundo semirufa	0	no	309	M > F	no	monogamy	animal	mixed	open	81, 82, 84
Junco hyemalis	0.5	yes	204	M > F	yes	monogamy	mixed	mixed	open	4, 99
Junco vulcani	0	no	28	—	no	—	mixed	mixed	open	4, 99

Social species whiter: flash marks absent in both species

Rhea americana	1.5	no	40 000	M > F	yes	polygyny	vegetable	passive	open	1, 6, 7, 8, 9, 10
Apteryx australis	0	no	2 000	M < F	no	monogamy	animal	passive	closed	1, 11
Egretta thula	5	no	400	M > F	no	monogamy	animal	active	open	12,13,14,15,16
Egretta sacra	0	no	400	M > F	no	monogamy	animal	active	open	4, 11, 12
Ardea alba	5	no	969	M > F	no	monogamy	animal	active	open	11, 12, 13, 14
Tigriornis leucolophus	0.5	no	500	M > F	yes	—	animal	active	closed	12, 13, 18
Ardea picata	1	no	264	M > F	no	monogamy	animal	active	open	4, 12, 13
Ardea sumatrana	0.5	no	2 000	M = F	no	monogamy	animal	active	open	4, 12, 13
Pelecanus onocrotalus	4	no	11 000	M > F	no	monogamy	animal	active	open	2, 18, 20
Balaeniceps rex	0	no	6 700	M > F	no	monogamy	animal	active	open	4, 18, 19, 20
Sula bassana	4	no	2 932	M = F	no	monogamy	animal	active	open	2, 14, 20
Sula leucogaster	1	no	917	M = F	no	monogamy	animal	active	open	2, 14, 18, 20
Chloephaga melanoptera	4	no	3 000	M > F	no	monogamy	vegetable	passive	open	22, 25
Cyanochen cyanopetrus	0.5	no	2 100	M > F	no	monogamy	vegetable	passive	closed	18, 22, 25
Anas erythrorhyncha	0.5	no	591	M > F	no	monogamy	mixed	passive	open	18, 21, 22, 28
Anas bahamensis	0.375	no	504	M > F	yes	monogamy	vegetable	passive	open	21, 22
Oxyura leucocephala	1.5	no	737	M > F	yes	monogamy	mixed	passive	open	2, 22, 32, 33
Oxyura maccoa	0	no	820	M > F	yes	polygyny	mixed	passive	open	22, 33, 34, 35
Oxyura jamaicensis	1.25	no	550	M > F	yes	monogamy	mixed	passive	open	22, 32, 33, 36
Biziura lobata	0	no	2 398	M > F	yes	monogamy	mixed	passive	open	11, 22, 33
Pandion haliaetus	1.5	no	1 428	M < F	yes	monogamy	animal	active	open	37, 38, 41, 42
Terathopius ecaudatus	1.125	no	2 000	M < F	yes	monogamy	animal	passive	open	37, 38
Haliaeetus leucocephalus	1	no	4 130	M < F	no	monogamy	animal	active	open	4, 37, 38
Aquila chrysaetos	0	no	3 572	M < F	no	monogamy	animal	active	open	37, 38, 42
Neophron percnopterus	4	no	1 889	M = F	no	monogamy	animal	passive	open	18, 38, 42, 43, 44
Gypaetus barbatus	0	no	5 755	M = F	no	monogamy	animal	passive	open	18, 38, 42, 43, 44
Gyps fulvus	0.25	no	7 436	M = F	no	monogamy	animal	passive	open	4,18,38,42,43,44
Aegypius monachus	0	no	9 700	M = F	yes	monogamy	animal	passive	open	2, 38, 44
Falco naumanii	1	no	131	M < F	yes	monogamy	animal	mixed	open	4, 38, 42, 46
Falco tinnunculus	0.5	no	109	M < F	yes	monogamy	animal	active	open	38, 42, 46

Appendix—*cont.*

Species[a]	Plumage score	Flash marks	Male body mass (g)	Size dimorphism	Dichromatic plumage	Mating system	Diet	Prey type	Habitat	References[b]
Pachyptila vittata	2.5	no	190	M = F	no	monogamy	animal	active	open	11, 58, 59
Pelecanoides georgicus	2	no	121	M = F	no	monogamy	animal	active	open	11, 58, 59
Platycercus eximius	0.5	no	1 086	M > F	yes	monogamy	vegetable	passive	mixed	69, 70, 71
Strigops habroptilus	0	no	2 000	M > F	no	lekking	vegetable	passive	closed	69, 70, 71
Merops apiaster	0.25	no	63	M > F	no	monogamy	animal	mixed	open	67, 73, 74
Merops pusillus	0	no	14	M = F	no	monogamy	animal	mixed	open	73, 74
Carpodectes hopkei	2.5	no	—	M > F	yes	lekking	vegetable	passive	closed	93, 94, 95
Lipaugus cryptolophus	0	no	—	M = F	no	—	animal	mixed	closed	93, 94, 95
Parus bicolor	1	no	216	M > F	no	monogamy	vegetable	passive	closed	101, 104, 106
Parus inortatus	0	no	159	—	no	monogamy	mixed	mixed	closed	101, 104
Social species whiter: flash marks present in non-social species only										
Ciconia ciconia	3	no	3 571	M > F	no	monogamy	animal	mixed	open	2, 18, 19
Ciconia nigra	1	yes	3 200	M > F	no	monogamy	animal	active	closed	2, 18, 19
Aix sponsa	1.25	no	680	M > F	yes	monogamy	vegetable	passive	open	21, 22, 23, 24
Cairina moschata	0.5	yes	2 915	M > F	no	monogamy	mixed	mixed	open	4, 21, 22
Anas rubripes	1	no	1 400	M > F	yes	monogamy	mixed	passive	open	4, 21, 22, 23
Anas sparsa	0	yes	—	M > F	no	monogamy	mixed	passive	closed	4, 18, 21, 22
Social species whiter: flash marks present in both species										
Malacorhynchus membranaceus	1	yes	404	M > F	no	monogamy	animal	mixed	open	11, 22, 26
Salvadorina waiguensis	0.75	yes	462	M = F	no	monogamy	animal	mixed	closed	22, 26
Nettapus coromandelianus	2	yes	403	M > F	yes	monogamy	vegetable	passive	open	11, 22, 26
Nettapus pulchellus	1.5	yes	310	M = F	yes	monogamy	vegetable	passive	open	11, 22, 26
Mergus merganser	2.375	yes	1 689	M > F	yes	monogamy	animal	active	open	2, 22, 30, 31
Mergus squamatus	0.5	yes	—	M > F	no	monogamy	animal	active	closed	4, 22, 31
Tringa erythropus	1.5	yes	142	M < F	no	monogamy	animal	passive	open	34, 47, 49
Tringa melanoleuca	1	yes	164	M < F	no	monogamy	animal	passive	open	47, 49, 52

Fulica rubifrons	0.5	yes	685	M > F	no	monogamy	vegetable	passive	open	61, 64
Fulica gigantea	0	yes	2 700	M > F	no	monogamy	vegetable	passive	open	61, 64
Pterocles alchata	1.5	yes	315	M > F	yes	monogamy	vegetable	passive	open	34, 66, 67
Pterocles lichtensteinii	0.5	yes	217	M > F	yes	monogamy	vegetable	passive	open	34, 66, 67
Anthracoceros coronatus	1.5	yes	—	M > F	yes	monogamy	mixed	passive	closed	72
Anthracoceros malayanus	0	yes	1 050	M > F	yes	monogamy	mixed	passive	closed	72
Aceros undulatus	0.875	yes	2 515	M > F	yes	monogamy	mixed	mixed	closed	72
Aceros nipalensis	0.25	yes	2 500	M > F	yes	monogamy	vegetable	passive	closed	72
Ceratogymna bucinator	0.5	yes	721	M > F	yes	monogamy	mixed	passive	closed	72, 73
Ceratogymna elata	0.25	yes	2 100	M > F	yes	monogamy	mixed	passive	closed	72, 73
Hemiprogne mystacea	1	yes	72	M < F	yes	monogamy	animal	mixed	open	75, 76
Hemiprogne comata	0.75	yes	70	—	yes	monogamy	animal	mixed	open	75, 76
No difference in white plumage: flash marks in social species only										
Struthio camelus	0.5	yes	83 000	M > F	yes	polygyny	vegetable	passive	open	1, 2
Cryptorellus boucardi	0.5	no	418	—	yes	monogamy	mixed	passive	closed	1, 3, 4, 5
Bostrychia caruncula	0	yes	1 500	—	no	monogamy	animal	mixed	open	18, 19
Bostrychia olivacea	0	no	1 500	—	no	monogamy	animal	mixed	closed	18, 19
Anas platyrhynchos	0.5	yes	1 088	M > F	yes	monogamy	mixed	mixed	open	2, 21, 22, 23
Anas laysanensis	0.5	no	456	M = F	no	monogamy	animal	mixed	open	21, 27
Vanellus cayanus	1.5	yes	72	M < F	no	—	animal	mixed	open	47, 49
Phegornis mitchelli	1.5	no	30	M < F	no	—	animal	mixed	open	47, 49
Phaps histronica	0.5	yes	293	M > F	yes	monogamy	vegetable	passive	open	51, 68
Phaps chalcoptera	0.5	no	344	M > F	yes	monogamy	vegetable	passive	mixed	51, 68
Urocissa whiteheadi	0.5	yes	—	—	no	monogamy	animal	mixed	closed	88, 89, 91
Cissa chinensis	0.5	no	132	M > F	no	monogamy	animal	mixed	closed	88, 89, 91
No difference in white plumage: flash marks absent in both species										
Anas chlorotis	0	no	580	M > F	yes	monogamy	animal	mixed	open	11, 21, 22
Anas aucklandica	0	no	550	M > F	no	monogamy	animal	mixed	open	4, 11, 21, 22
Neophema elegans	0	no	434	M > F	yes	monogamy	vegetable	passive	mixed	69, 70, 71
Pezoporus wallicus	0	no	757	—	no	monogamy	vegetable	passive	open	69, 70, 71

Appendix—*cont.*

Species[a]	Plumage score	Flash marks	Male body mass (g)	Size dimorphism	Dichromatic plumage	Mating system	Diet	Prey type	Habitat	References[b]
Synthliboramphus antiqus	2	no	242	M = F	no	monogamy	animal	active	open	77, 78
Synthliboramphus hypoleucus	2	no	164	M = F	no	monogamy	animal	active	open	77, 78, 79
Riparia riparia	1	no	135	M = F	no	monogamy	animal	mixed	open	81, 82, 84, 85
Riparia cincta	1	no	223	M = F	no	monogamy	animal	mixed	open	81, 84, 85
Turdus iliacus	0.5	no	696	M = F	no	monogamy	mixed	passive	open	85, 86
Turdus libonyanus	0.5	no	556	M = F	no	monogamy	mixed	passive	open	86
Gymnorhinus cyanocephalus	0	no	103	M > F	no	monogamy	mixed	passive	closed	87, 88, 89, 90, 91
Cyanocitta stelleri	0	no	128	M > F	no	monogamy	mixed	passive	closed	87, 88, 89, 90, 91
Ptilostomus afer	0	no	128	—	no	monogamy	animal	mixed	open	88, 89, 91
Perisoreus infaustus	0	no	876	M > F	no	monogamy	mixed	mixed	closed	88, 89, 91, 92
Cacicus cela	0	no	105	M > F	yes	polygyny	mixed	passive	closed	4, 96
Cacicus solitarius	0	no	90	M > F	no	—	animal	mixed	closed	4, 96
Icterus spurius	0	no	21	M > F	yes	monogamy	mixed	passive	closed	96, 97, 98
Icterus chrysocephalus	0	no	41	M > F	no	monogamy	animal	mixed	closed	4, 96, 97
Agelaius thilius	0	no	30	M > F	yes	monogamy	mixed	passive	open	4, 96
Agelaius xanthophthalmus	0	no	45	M > F	yes	—	mixed	mixed	open	4, 96
Sitta pygmaea	0.5	no	106	M = F	no	monogamy	vegetable	passive	closed	4, 100, 101
Sitta canadensis	0.5	no	11	M > F	yes	monogamy	vegetable	passive	closed	100, 101, 102
Parus hudsonicus	1	no	98	M = F	no	monogamy	mixed	passive	closed	101, 103, 104
Parus lugubris	1	no	175	—	yes	monogamy	mixed	mixed	closed	101, 104, 105
Aplonis metallica	0	no	61	M = F	no	monogamy	mixed	passive	closed	107
Aplonis grandes	0	no	—	M = F	no	monogamy	mixed	passive	closed	107
No difference in white plumage: flash marks in non-social species only										
Pluvialis apricaria	1.5	no	196	M = F	no	monogamy	animal	passive	open	47, 49, 50
Pluvialis squatarola	1.5	yes	217	M = F	no	monogamy	animal	passive	open	47, 49, 50, 55
Vanellus vanellus	1	no	192	M > F	no	monogamy	animal	passive	open	47, 49, 50
Vanellus crassirostris	1	yes	198	M > F	no	monogamy	animal	mixed	open	34, 47, 49

No difference in white plumage: flash marks present in both species										
Aythya australis	1.5	yes	902	M > F	yes	monogamy	mixed	mixed	open	11, 22, 29
Aythya nyroca	1.5	yes	589	M > F	yes	monogamy	vegetable	passive	open	2, 22, 29
Porphyrio porphyrio	0	yes	868	M > F	no	polygyny	vegetable	passive	open	34, 42, 56, 61, 64
Porphyrio mantelli	0	yes	2 673	M > F	no	monogamy	vegetable	passive	mixed	42, 61, 64
Mina dumontii	0.5	yes	217	M = F	no	monogamy	mixed	passive	closed	107
Mina kreffti	0.5	yes	—	—	no	monogamy	vegetable	passive	closed	107
Social species less white: flash marks present in social species only										
Parabuteo unicinctus	0.5	yes	690	M < F	no	monogamy	animal	active	open	37, 38, 39
Buteo jamaicensis	1.5	no	1 028	M < F	no	monogamy	animal	active	open	37, 38, 40
Social species less white: flash marks absent for both species										
Egretta caerulea	0	no	364	M > F	no	monogamy	animal	active	open	12, 13, 17
Egretta novaehollandiae	1	no	599	M > F	no	monogamy	animal	active	open	12, 13
Pygoscelis adeliae	2	no	5 350	M > F	no	monogamy	animal	active	open	11, 57, 58
Eudyptula minor	2.5	no	1 063	M > F	no	monogamy	animal	active	open	11, 57, 58
Puffinus griseus	0.5	no	787	M = F	no	monogamy	animal	active	open	11, 58, 59
Puffinus assimilis	2	no	177	M = F	no	monogamy	animal	active	open	11, 58
Grus grus	0.5	no	5 750	M > F	no	monogamy	vegetable	passive	open	34, 42, 61, 63
Grus americana	4	no	7 496	M > F	no	monogamy	mixed	mixed	open	61, 62, 63
Aethia cristatella	0.5	no	268	M > F	no	monogamy	animal	active	open	77, 78
Cyclorhynchus psittacula	1.5	no	292	M > F	no	monogamy	animal	active	open	77, 78
Social species less white: flash marks present in non-social species only										
Ictinia mississipiensis	0	no	245	M < F	yes	monogamy	animal	mixed	open	37, 38, 45
Spilornis cheela	0.5	yes	900	M < F	no	monogamy	animal	active	closed	4, 37, 38
Corvus monedula	0	no	256	M > F	no	monogamy	mixed	passive	open	88, 89, 91, 92
Nucigraga caryocatactes	0.5	yes	198	M > F	no	monogamy	vegetable	passive	closed	88, 89, 91, 92
Acridotheres gingianianus	0	no	70	M > F	no	monogamy	mixed	mixed	closed	107
Acridotheres tristis	0.5	yes	127	M > F	no	monogamy	mixed	mixed	closed	107

Appendix—*cont.*

Species[a]	Plumage score	Flash marks	Male body mass (g)	Size dimorphism	Dichromatic plumage	Mating system	Diet	Prey type	Habitat	References[b]
Social species less white: flash marks present for both species										
Glareola pratincola	0.5	yes	79	M > F	no	monogamy	animal	mixed	open	34, 47, 49
Rhinoptilus cinctus	1.5	yes	125	M = F	no	monogamy	animal	mixed	open	34, 47, 49
Garrulus lidthi	0.25	yes	—	—	no	monogamy	mixed	passive	closed	88, 89, 91
Garrulus glandarius	0.5	yes	172	M > F	no	monogamy	mixed	passive	closed	88, 89, 91, 92

[a] The first species of each pair represents the social foraging species and the second the solitary species.

[b] *References*: 1, Van Tuinen *et al.* (1998); 2, Cramp and Simmons (1977); 3, Lancaster (1964); 4, Dunning (1993); 5, Stiles and Skutch (1989); 6, Martella *et al.* (1996); 7, Reboreda and Fernandez (1997); 8, Fernandez and Reboreda (1998); 9, Bruning (1974); 10, Blake (1977); 11, Marchant and Higgins (1990); 12, McCraken and Sheldon (1998); 13, Hancock and Elliot (1978); 14, Palmer (1962a); 15, Smith (1995); 16, Caldwell (1981); 17, Rodgers and Smith (1995); 18, Brown *et al.* (1982); 19, Hancock *et al.* (1992); 20, Hedges and Sibley (1994); 21, Livezey (1991); 22, Johnsgard (1978); 23, Palmer (1962b); 24, Hepp and Bellrose (1995); 25, Livezey (1997a); 26, Livezey (1997b); 28, Moulton and Marshall (1998); 28, Bricknell (1982); 29, Livezey (1996); 30, Mallory and Metz (1999); 31, Livezey (1995a); 32, Johnsgard and Carbonell (1996); 33, Livezey (1995b); 34, Urban *et al.* (1986); 35, Clark (1964); 36, Palmer (1976); 37, Griffiths (1994); 38, Brown and Amadon (1968); 39, Bednarz (1995); 40, Preston and Beane (1993); 41, Poole (1989); 42, Cramp and Simmons (1980); 43, Mundy *et al.* (1992); 44, Seibold and Helbig (1995); 45, Parker (1999); 46, Griffiths (1999); 47, Chu (1995); 48, Whittingham *et al.* (2000); 49, Hayman *et al.* (1986); 50, Cramp and Simmons (1983); 51, Marchant and Higgins (1996); 52, Elphick and Tibbits (1998); 53, Andersson (1999); 54, Furness (1987); 55, Paulson (1995); 56, Marchant and Higgins (1993); 57, Williams (1995); 58, Paterson *et al.* (1995); 59, Bretagnolle (1993); 60, Weimerskirch *et al.* (1986); 61, Livezey (1998); 62, Lewis (1995); 63, Johnsgard (1983); 64, Taylor (1998); 65, Johnsgard (1986); 66, Johnsgard (1991); 67, Cramp (1985); 68, Goodwin (1983); 69, Higgins and Davies (1999); 70, Juniper and Parr (1998); 71, Leeton *et al.* (1994); 72, Kemp (1995); 73, Fry *et al.* (1988); 74, Fry and Fry (1992); 75, Chantler and Driessens (1995); 76, Lee *et al.* (1996); 77, Gaston and Jones (1998); 78, Moum *et al.* (1994); 79, Drost and Lewis (1995); 80, Brown and Toft (1999); 81, Sheldon and Winkler (1993); 82, Turner (1989); 83, Brown and Brown (1995); 84, Keith *et al.* (1992); 85, Cramp (1988); 86, Urban *et al.* (1997); 87, Cibois and Pasquet (1999); 88, de los Monteros and Cracraft (1997); 89, Goodwin (1986); 90, Marzluff and Balda (1992); 91, Madge and Burn (1994); 92, Cramp and Perrins (1994); 93, Snow (1982); 94, Ridgely and Tudor (1989); 95, Prum *et al.* (2000); 96, Jaramillo and Burke (1999); 97, Omland *et al.* (1999); 98, Scherf and Kren (1996); 99, Byers *et al.* (1996); 100, Pasquet (1998); 101, Harrap and Quinn (1995); 102, Ghalambor and Martin (1999); 103, Ficken *et al.* (1996); 104, Slikas *et al.* (1996); 105, Cramp and Perrins (1993); 106, Grubb and Pravasudov (1994); 107, Feare and Craig (1998).