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A comparative study of breeding traits in colonial birds

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ABSTRACT

I examined the effect of an evolutionary transition to coloniality on several breeding traits in birds using 29 pairs of congeners that included one colonial and one solitary breeding species. Males in colonial and solitary species, as well as females, had similar body masses. The extent to which the sexes differed in body mass and plumage characteristics was also similar in colonial and solitary species. Although sexual selection is often assumed to be stronger in colonial species, coloniality appears to be a weak force in the sexual diversification of body mass and plumage characteristics in birds. Colonial species produced heavier eggs and invested more in their offspring per unit of female body mass than their solitary counterpart. The results support the hypothesis that coloniality is associated with greater foraging efficiency, which allows colonial birds to increase parental effort. Although offspring predation risk is often assumed to be smaller in colonial species, a fact that could lead to the production of larger clutches, colonial and solitary species produced clutches of similar size. The results thus provide little support for an effect of differential predation pressure on changes in clutch size in colonial species.

Keywords: birds, clutch size, colonial breeding, egg mass, pairwise comparative method.

INTRODUCTION

Birds across several taxa gather to nest in a centralized area from which they depart regularly in search of food. The occurrence and ecological correlates of colonial breeding in birds are well known (Crook, 1964; Lack, 1968; Wittenberger and Hunt, 1985; Siegel-Causey and Kharitonov, 1990). Controversy has centred upon the adaptive value of coloniality. Birds are generally thought to benefit from colonial breeding through enhanced foraging efficiency and reduced predation risk. Nevertheless, several factors can mitigate against the beneficial nature of colonies, including increased risk of disease, ectoparasite transmission and cuckoldry (Wittenberger and Hunt, 1985).

Bird species in a colonial environment can thus face different ecological realities to similar species breeding solitarily. However, little attention has been paid to potential adjustments in breeding traits following the evolutionary transition to coloniality. For instance, it has been suggested that colonial birds might be under stronger sexual selection (Mooers and Møller, 1996), a fact that could lead to sexual differences in traits such as body

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mass and plumage characteristics. In addition, the purported changes in foraging efficiency and predation risk might allow colonial birds to alter breeding traits such as clutch size and egg mass (Martin, 1995). In the following, I compare pairs of congeners that include one colonial and one solitary breeding species to examine potential adjustments to coloniality in several breeding traits. Comparisons between pairs of closely related species have long been recognized as a powerful tool to examine changes in behavioural and morphological traits in response to variation in social organization (Orians, 1961; Tinbergen, 1963; Møller and Birkhead, 1992).

PREDICTIONS

I detail here a series of predictions regarding the direction of potential changes in the breeding traits of colonial birds. Potential changes are examined with respect to three factors: sexual selection intensity, foraging efficiency and predation risk.

Sexual selection

Several lines of evidence suggest that birds living in colonies are under stronger sexual selection. For instance, the rate of extra-pair copulations is higher in colonial species than in closely related solitary species (Wittenberger and Hunt, 1985; Møller and Birkhead, 1992). Because of high variance in male mating success, we might expect the development of heritable cues in males that could be useful in competition over mates. Features such as sexual plumage dichromatism and sexual dimorphism in body size and feather characteristics are often invoked as potential cues in mate choice (Andersson and Iwasa, 1996). The extent to which the sexes differ in these features could thus be expected to be greater in colonial species than in closely related solitary species.

Foraging efficiency

Two opposite predictions can be derived from our knowledge of foraging efficiency in colonial birds. First, competition for food has sometimes been predicted to be greater in colonial than in solitary species (Wittenberger and Hunt, 1985). Support for the hypothesis comes from studies showing that several breeding traits, including egg mass and clutch size, are depressed in larger colonies of the same species (Hunt *et al*., 1981; Coulson *et al*., 1982). If competition for food is indeed more intense in colonial species, we might expect egg mass and clutch size in colonial species to be smaller than that in closely related solitary species.

On the other hand, several mechanisms have been hypothesized to increase foraging efficiency in colonial birds. For instance, unsuccessful colony members might be able to follow successful foragers to rich patches of food (Ward and Zahavi, 1973; Beauchamp and Lefebvre, 1988; Barta and Szep, 1995). The colony might also act as a recruiting centre from which individual colony members entice other birds to join their food discoveries, thereby providing benefits associated with larger feeding group sizes (Richner and Heeb, 1997). In addition, the high spatial concentration of foragers that occurs around colonies might allow individuals to join the food discoveries of others more rapidly (Buckley, 1997). All these factors, in contrast to the hypothesis of increased food competition, would allow an increase in foraging efficiency and presumably an increase in the amount of energy that can

be allocated to parental effort. The end result could be reflected in larger clutch sizes and/or larger egg masses.

Predation risk

Several studies indicate that predation on eggs or nestlings is reduced when colony size increases, presumably as a consequence of swamping and mobbing effects (Wittenberger and Hunt, 1985; Johnsson, 1994; Wicklund and Andersson, 1994; Becker, 1995; Soler and Soler, 1996). Current life-history theory predicts that increases in offspring survival might allow parent birds to lay larger clutches (Martin, 1995). Therefore, clutch size in colonial species might be expected to be larger than that in solitary species. The above life-history paradigm fails to make a direct prediction with respect to egg mass. Energy trade-offs during reproduction, if food availability remains constant, would predict that, as clutch size increases, egg mass would probably decline.

METHODS

I searched the ornithological literature for pairs of congeners that included one colonial and one solitary species. I used the definition of coloniality proposed by Wittenberger and Hunt (1985) to assess nesting dispersion. Coloniality requires that individuals nest in a more or less centralized location from which they depart regularly in search of food. Foraging thus occurs away from the colony. Based on the available evidence, I distinguished two types of nesting dispersion: solitary and colonial. Some species showed a continuum of nesting dispersion, from solitary to colonial breeding. For the purpose of the analysis, I classified these species among the colonial nesters.

I used several criteria to choose among the possible pairs of related species. If a phylogenetic tree of the family including the congeners existed, I chose pairs of sister species that differed with respect to nesting dispersion. If a phylogenetic analysis was lacking, I chose species so that each member of a pair belonged to the same genus. Here, the choice of a colonial species was usually simple, as coloniality is not widespread in birds. From the same genus, I chose a solitary counterpart that ideally lived in the same geographical area and provided sufficient data to evaluate the dependent breeding traits. If more than one solitary species was available, I chose that pair member randomly.

For each species, I recorded information on the following traits: average male and female body mass (g), plumage differences between the sexes, clutch size and egg mass (g). I scored a value of 1 when males and females showed differences in plumage coloration or feather characteristics, and a value of zero otherwise. In some species, egg mass had not been estimated directly, although egg dimensions were provided. In this case, I used known allometric relationships between egg volume and egg mass to estimate egg mass indirectly (Paganelli *et al.*, 1981). Because egg mass is correlated with female mass, I used a corrected value (%) by dividing egg mass by average female body mass. I calculated sexual size dimorphism by dividing average male mass by average female mass. Finally, I defined parental effort (%), a measure of the energy allocated to reproduction, as the product of clutch size and egg mass divided by average female mass.

For each pair of congeners, I calculated the difference between values of each variable for the colonial species and non-colonial counterparts. Under the null hypothesis of no difference between colonial and solitary species, the expected rank sums would be the same

Table 1. Differences in traits across 29 pairs of birds with contrasting nesting dispersion

Traits	Mean difference (S.D.)	Wilcoxon's T	P
Male mass (g)	57.7 (669.7)	201	0.73
Female mass (g)	–27.2 (382.7)	214	0.52
Sexual dimorphism	0.041 (0.18)	187.5	0.24
Plumage dichromatism	–0.035 (0.42)	216	0.50
Clutch size	0.20 (1.21)	199.5	0.28
Corrected egg mass (%)[a]	11.7 (12.0)	0	0.0001
Parental effort (%)	3.8 (11.6)	103	0.0055

[a] Corrected for female mass.

for the positive and negative differences. I evaluated the null hypothesis with Wilcoxon's signed-ranks test (Sokal and Rohlf, 1995). I used one-tailed tests when evaluating the above hypotheses, and two-tailed tests otherwise.

RESULTS

I found 29 pairs of congeners across a wide variety of taxa that differed with respect to nesting dispersion (Appendix).

Sexual selection

Males in each pair, as well as females, showed no difference in average body mass (Table 1). Although sexual size dimorphism was pronounced in some species (e.g. *Circus* sp., *Falco* sp.), the extent to which the sexes differed in body mass was similar in colonial and solitary species (Table 1). Plumage differences between the sexes occurred in seven colonial species (Appendix). In this subset of species, five of the seven solitary congeners also showed similar qualitative differences in plumage. Moreover, three solitary species showed plumage differences between the sexes, whereas their colonial counterparts failed to exhibit any differences. Across all pairs, the extent to which the sexes differed in plumage characteristics was similar in colonial and solitary species (Table 1).

Foraging efficiency and predation risk

Colonial and solitary species laid clutches of similar sizes (Table 1). On the other hand, colonial species produced heavier eggs, corrected for average female mass, than their solitary counterparts (Table 1). As measured by the parental effort index, females breeding colonially also invested relatively more in their offspring than their solitary congeners (Table 1).

DISCUSSION

Comparisons between pairs of closely related species are useful to examine potential adjustments in dependent traits following an evolutionary transition in an independent

variable such as social organization (Møller and Birkhead, 1992). This is especially true when the number of taxa included in the study is large and phylogenies are poorly known. In pairwise comparisons, the choice of closely related species reduces the possibility that confounding factors have changed simultaneously with the transition in the independent variable of interest. Use of the pairwise comparison method in my study revealed changes in some breeding traits following the transition to coloniality in birds, but also a lack of effect in other traits.

Sexual selection

Although the intensity of sexual selection has been hypothesized to be stronger in colonial species, I found little evidence for more differences between the sexes in body mass and plumage characteristics in colonial species than in solitary species. Similarly, Mooers and Møller (1996) failed to find evidence for a greater rate of speciation in colonial bird taxa despite the fact that the intensity of sexual selection was predicted to increase the rate of speciation.

It is conceivable that differences in body mass and plumage characteristics between the sexes reflect processes that are not related to sexual selection. For instance, sexual size dimorphism in raptors has been linked to differences in foraging ecology between the sexes (Ydenberg and Forbes, 1991). Although sexual differences in body mass and plumage characteristics occurred in several colonial species, their solitary counterparts also frequently exhibited similar differences. It appears that the evolutionary transition to coloniality in birds often happened after the development of these sexual differences. Therefore, coloniality does not seem to be a force that generates sexual diversity in mass and plumage characteristics of birds.

Foraging efficiency

I failed to find support for the hypothesis that competition for food is greater in colonial species. In fact, clutch size and egg mass, which are often considered reliable indicators of competition intensity, were not smaller in colonial species. The evidence in support of the competition hypothesis is usually based on intraspecific studies. Therefore, the true relationship between breeding traits and colony size may be confounded by factors that co-vary with both, such as parental quality or food distribution (Wittenberger and Hunt, 1985; Ainley *et al*., 1995). The pairwise comparison method is not hindered by such confounding tendencies and is more suitable to investigate adjustments in breeding traits.

In contrast to the above prediction, female colonial breeders laid heavier eggs with respect to their body mass than their solitary counterparts. Parental effort, per unit female body mass, also increased in colonial species. Because colonial and solitary species produced clutches of similar sizes, the increase in parental effort was mostly due to the relative increase in egg mass. The results thus support the hypothesis that colonial breeding can enhance foraging efficiency. Increases in food intake would allow colonial breeders to invest more in their offspring by producing heavier eggs. The positive relationship between egg production and the nutritional status of breeders is well documented (Monaghan and Nager, 1997), and could serve as a physiological mechanism allowing production of heavier eggs.

It is not clear why the transition to coloniality failed to alter clutch size appreciably. Within a species, colonial breeding can sometimes lead to the production of larger clutches (Bukacinska *et al*., 1993), but the evidence is scarce across species. Martin (1995) reported little difference in clutch size across species that use habitats or foraging sites which probably differ greatly in food availability. It appears as though clutch size is a trait that shows little flexibility in response to changes in foraging efficiency across species.

Although the results suggest greater foraging efficiency in colonial birds, it is impossible to specify which foraging mechanism is involved. A challenge for future studies would be to investigate the foraging behaviour of closely related species and pinpoint which mechanisms might allow colonial species to achieve greater foraging efficiency. It is also important to bear in mind that a greater foraging efficiency may not translate into a greater reproductive success in colonial species. Although colonial species lay heavier eggs, and thus produce presumably larger offspring, several factors – such as rate of ectoparasite infestation, which can be higher in colonial species – can reduce growth rate and offspring survival (Brown and Brown, 1986).

Predation risk

The decrease in offspring predation risk that has been observed in several studies of colonial birds failed to translate into an appreciable increase in clutch size as predicted by current life-history theory (Martin, 1995). It is possible that the decrease in offspring predation risk that was achieved during the transition to coloniality was too small to affect clutch size substantially. In support of this idea, other studies have shown large effects of predation risk on clutch size in passerine birds (Martin, 1995). Traits such as number of broods have also been shown to be affected by predation risk (Martin, 1995). It is therefore possible that the decrease in predation risk that occurred during the evolution of coloniality affected clutch size to a lesser extent than other factors, such as number of broods. This possibility remains to be investigated.

The lack of an effect of coloniality on clutch size can also be interpreted differently. Factors that are unrelated to predation risk or foraging efficiency might mitigate against the trend of increasing clutch size. Poiani (1993) presented comparative evidence suggesting that a high rate of ectoparasite infestation can lead to the production of smaller clutches in birds. Because colonial birds often experience higher rates of infestation (Wittenberger and Hunt, 1985; Brown and Brown, 1986), parasitism may have a negative effect on clutch size that counterbalances the expected positive trend. It remains to be shown whether a high rate of ectoparasite infestation is common enough across the bird taxa involved in this study to account for the lack of effect of clutch size.

In conclusion, the evolutionary transition to coloniality in birds appears to have caused an increase in egg mass and greater levels of parental effort, probably as a consequence of enhanced foraging efficiency. The results support the idea that foraging efficiency played an important role in the evolution of coloniality in birds (Clode, 1993). On the other hand, coloniality seems to have a weaker effect on clutch size and on sexual differences in body mass and plumage characteristics. Future studies could extend the use of the pairwise method to other traits that are suspected to co-vary with coloniality (Wittenberger and Hunt, 1985). Traits such as ectoparasite infestation and physiological adaptations to food stress in nestlings offer the chance to examine further the extent to which coloniality influenced the expression of breeding traits in birds.

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Appendix

Attributes for pairs of birds as a function of contrasting nesting dispersion.

Species	Male mass (g)	Female mass (g)	P.D.[a]	Egg mass (g)	Clutch size	Reference[b]
Dendrocygna autumnalis (S/C)[c]	816	839	0	44	14	1, 2
Dendrocygna viduata (S)	686	662	0	36	10	1, 2
Dendrocygna bicolor (S/C)	675	690	1	50	12	1, 2
Dendrocygna eytoni (S)	788	792	1	40	11	1, 2
Cygnus atratus (S/C)	6270	5100	0	300	6	1
Cygnus melanocoryphus (S)	5400	4000	0	247	6	1
Branta canadensis (S/C)	5166	2595	0	127	5	1
Branta sanvicensis (S)	2212	1923	0	143	4.6	1
Anser caerulescens (C)	2180	1952	0	125	4.5	3
Anser fabalis (S)	3198	2843	0	146	5	4
Somateria mollissima (C)	2000	1500	1	110	5	1
Somateria spectabilis (S)	1830	1750	1	73	5	1
Aythya marila (C)	997	907	1	61	9.73	1
Aythya affinis (S)	861	770	1	49.5	10	1
Milvus migrans (S/C)	807	850	0	56	2.5	5
Milvus milvus (S)	947	1213	0	63	2	5
Pandion halieatus (S/C)	1428	1627	0	72	2.6	5
Terathopius ecaudatus (S)	2348	2348	0	164	1	6, 7, 8
Circus pygargus (S/C)	261	370	0	25	4.2	5
Circus macrourus (S)	322	445	1	28	4.5	5
Haliastur sphenurus (S/C)	618	870	0	54	2	9
Haliastur indus (S)	536	626	0	47	1.5	9
Falco naumanni (C)	131	175	1	16	3.8	5
Falco columbarius (S)	162	212	1	21.5	3.96	5
Podiceps nigricollis (C)	334	256	0	21	3.5	4
Podiceps auritus (S)	424	384	1	23	4.5	4
Vanellus leucorus (C)	128	128	0	16.2	4	10
Vanellus malabaricus (S)	156	156	0	13.5	4	10
Limosa limosa (S/C)	360	425	1	37	4	10
Limosa haemastica (S)	221.8	289	0	37.5	4	10
Limnodromus semipalmatus (C)	181	190	0	26.8	2	10
Limnodromus scolopaceus (S)	99.9	114.7	0	17.5	4	10

Appendix *continued*

Species	Male mass (g)	Female mass (g)	P.D.[a]	Egg mass (g)	Clutch size	Reference[b]
Himantopus himantopus (S/C)	193	192	0	24	3.7	11
Himantopus novaezelandiae (S)	219	227	0	25	4	11, 12
Ciconia ciconia (S/C)	3571	3325	0	111	4	4
Ciconia nigra (S)	3000	3000	0	86	4	4
Ardea alba (C)	969.2	761.3	0	36.5	3.5	11
Ardea novaehollandiae (S)	599.2	521.2	0	27.4	3.77	11
Gallinula ventralis (S/C)	410	364	0	36.1	5.9	11
Gallinula tenebrosa (S)	570	493	0	24.5	7.8	11
Pterocles alcheta (S/C)	250	225	1	24	2.5	13
Pterocles orientalis (S)	428	383	1	28	2.5	13
Columba livia (S/C)	294	267	0	18	2	13
Columba palumbus (S)	496	480	0	18.5	1.84	13
Turdus pilaris (S/C)	114.9	116.6	0	6.53	5.5	14
Turdus merula (S)	113.8	106.8	1	7.6	4	14
Pyrrhocorax gracilis (S/C)	210	210	0	14.1	4.2	15
Pyrrhocorax pyrrhocorax (S)	273	236.5	0	15.7	3.88	15
Corvus frugilegus (C)	489	418	0	16	4.5	15
Corvus corax (S)	1254	1147	0	28.8	4.5	15
Pica nuttali (C)	175	146.1	0	8.3	5.7	15
Pica pica (S)	234.6	210.4	0	9.9	5.8	15, 16
Hirundo rustica (C)	18.8	19.4	0	1.9	4.4	14, 17
Hirundo daurica (S)	22.1	22.4	0	2.01	4.13	14, 17
Riparia riparia (C)	13.5	13.5	0	1.43	5	17
Riparia cincta (S)	21.5	21.5	0	2.79	3.5	17
Merops apiaster (C)	55.7	53.8	1	6.3	5.8	18
Merops boehmi (S)	18.7	17.0	0	2.24	3	18

[a] P.D. = plumage differences between the sexes: 0 = absent, 1 = present.
[b] 1, Johnsgard (1978); 2, Livezey (1995); 3, Cooke *et al*. (1995); 4, Cramp and Simmons (1977); 5, Cramp and Simmons (1980); 6, Pickford *et al*. (1989); 7, Brown and Amadon (1968); 8, Griffiths (1994); 9, Marchant and Higgins (1993); 10, Johnsgard (1981); 11, Marchant and Higgins (1990); 12, Dunning (1993); 13, Cramp and Simmons (1983); 14, Cramp (1988); 15, Cramp and Perrins (1994); 16, Birkhead (1991); 17, Turner (1989); 18, Fry (1984).
[c] S = solitary breeder; C = colonial breeder; S/C = solitary to colonial breeder.