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Evolution of Coloniality in Waterbirds: Perspectives and Advances

Abstract

Colonial nesting in birds is a well documented ecological phenomenon. Despite considerable research, the understanding of the causal factors and maintenance of coloniality in birds is still limited. We did a qualitative review of the existing literature to summarize the recent progress in research on the evolution of avian coloniality. We examined the two major schools of thought, i.e., the phylogenetic and cost-and-benefit approaches that try to explain avian coloniality. A detailed review of the literature suggests that coloniality evolved several times in response to several interacting factors. However, more case studies are required to form a general framework of the evolution of coloniality.

Keywords : *Bird colony, breeding, foraging, information centre, waterbird*

Introduction

Coloniality is a type of social reproduction in which individuals breed within densely distributed nesting territories that contain no resources other than nesting sites (Perrins & Birkhead 1983). It has been reported in many faunal taxa such as fish(Fraipont *et. al.* 1993), reptiles (Trillmich & Trillmich 1986), mammals (Hayes 1999)and, most commonly, birds (Rolland *et al.* 1998). It is the second most common type of avian social organization after territoriality (Brown & Brown 2001). Lack (1968) estimated that 13–14% of all bird species (29 of 129 avian families) show colonial nesting (although his exact definition of a "colonial species" is unknown). However, Rolland *et al.*(1998) found 30% species to be colonial. This phenomenon is most significant in seabirds particularly, as it is seen in 98% of seabird species (Lack 1968,Wittenberger& Hunt 1985).

Colonial nesting in waterbirds is one of the least understood phenomena in avian biology (Brown & Brown 2001). Although a considerable amount of research has been done on the evolution of colonial nesting, it still remains an evolutionary puzzle. Among the various hypotheses proposed, none can be considered as a stand-alone explanation of the basic factors that gave rise to coloniality or the factors that maintain it in the present form. A general framework to explain the evolution and maintenance of coloniality is still lacking (Danchin & Wagner 1997). In this context, the purpose of this review paper is to summarize the various schools of thought about the evolution of coloniality in waterbirds and highlight recent progress in research on avian coloniality.

The study of coloniality is important to other aspects of avian biology also (Brown & Brown 2001). The pattern of spatial distribution in bird colonies can be easily studied, and so it can be used as a natural model to test hypotheses about natural selection (Horn 1968). It can also help us understand the evolution of group living of all social animals in general. Bird colonies present many opportunities to study parasite transmission and provide epidemiological models for human cities (Keeling & Grenfell 1997). Besides, they also provide a natural framework for investigating metapopulation biology (Hanski & Gilpin 1991), source–sink dynamics (Pulliam 1988) and population genetic structure.

Methods

We searched for published literature on avian coloniality in searchable databases available in the Web and libraries. In this paper, we have reviewed qualitatively the various schools of thought on the evolution of coloniality.

For the present study, we define waterbirds as a diverse group of birds that are ecologically tied to waterbodies and that are primarily and anatomically adapted to live in aquatic conditions during a partor the full duration of their life cycle (Owen & Black 1990). We followed Burger's (1981) definition of a bird colony, which states that it is a place where birds nest in close proximity to one another (or can see one another), interact regularly (many times a day) and do not feed within their territories but use them only for nesting activities.

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The study of coloniality is important to other aspects of avian biology also (Brown & Brown 2001). The pattern of spatial distribution in bird colonies can be easily studied, and so it can be used as a natural model to test hypotheses about natural selection (Horn 1968). It can also help us understand the evolution of group living of all social animals in general. Bird colonies present many opportunities to study parasite transmission and provide epidemiological models for human cities (Keeling & Grenfell 1997). Besides, they also provide a natural framework for investigating metapopulation biology (Hanski & Gilpin 1991), source–sink dynamics (Pulliam 1988) and population genetic structure.

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Results

Two major approaches have been followed to examine colonial nesting behaviour in birds. These are

- The phylogenetic approach (also called the transformational approach)
- The cost-and-benefit approach (equilibrium or economic framework).

Phylogenetic Approach

The phylogenetic approach examines coloniality within an evolutionary context. It analyses the phylogenetic patterns of similarities and differences across taxa to test evolutionary concepts. This approach can provide a way to answer how colonial breeding has evolved in relation to species structure, function and behaviour. For example, whether solitary or colonial breeding is the ancestral state in birds and how many times coloniality has evolved within a class (taxonomic rank) can be explored through this approach. Multiple evolutionary appearances of coloniality would suggest that particular ecological constraints (food distribution, extent of predation) led to the evolution of colonialty, whereas a limited number of evolutionary appearances would suggest that it is a phylogenetically constrained behaviour and has little relevance to species' current ecology (Brown & Brown 2001). Finding out the most probable pathway can help reveal the original selective pressures of coloniality (Brown & Brown 2001).However, this approach is limited by the lack of an accurate phylogeny and precise recognition of homology (Siegel-Causey & Kharitonov 1990). Still, it can be useful in estimating the selective forces for the evolution of coloniality by mapping the various social breeding systems in bird phylogeny.

Earlier studies on phylogenetic pattern of avian colonialty hypothesized that the most primitive social organization involves spatially isolated groups of individuals of the same sex, or leks; whereas colonial and communal breeding systems are considered socially and evolutionarily most developed. Siegel-Causey and Kharitonov (1990) examined the occurrence of colonial nesting across the major groups of birds by following the phylogenetic classification of Sibley *et*

al.(1988). They showed that coloniality has evolved independently in at least 10 different lineages of birds. This result suggests that different adaptive forces might have operated in different lineages of colonial breeding and so coloniality may serve different functions in unrelated groups of birds. Siegel-Causey and Kharitonov agreed with the earlier hypothesized pathways of evolution from individual to social breeding system. Therefore, coloniality is evolutionarily advanced compared with solitary nesting and loose aggregation of territorial nesters. Rolland *et al.*(1998) used the phylogeny of Sibley & Ahlquist (1990), based on DNA–DNA hybridization, and focused on three super-orders presenting different incidences of colonialty: the Apodimorphae, Strigimorphaeand Passerimorphae. Among the 55 families, containing 320 taxa, used for reconstruction of the evolution of coloniality, they found 208 solitary breeding (65%), 96 colonial (30%) and 16 polymorphic species (5%). Coloniality seemed to evolve independently at least 21 times on the study phylogenetic tree. They detected 10 reversals from colonial to solitary breeding also. In all the possible reconstructions of the evolution of coloniality, solitary breeding was found to be the ancestral state. Rolland *et al.* also deduced that the ancestral species defended a feeding territory and was terrestrial. The only evolutionary route from the ancestral solitary/terrestrial state to the derived colonial/aquatic state was estimated to be through an intermediate state in which species were solitary and aquatic. Colonial breeding appeared highly correlated with an absence of feeding territories, the aquatic habitat and nest exposure to predators, but it was not correlated with changes in life history traits (body mass and clutch size). Colonial species have been more prone to become marine, and coloniality significantly preceded the transition to the marine habitat. Rolland *et al.* found that a non-marine state favours the loss of feeding territoriality, which in turn favours the passage to a marine life. So it is not a marine life that forced species to become colonial, as is usually accepted, but rather it is colonial breeding that allowed species to exploit the marine environment, in which food is likely to be patchy and unpredictable for exploitation by solitary breeders. The only possible pathway from the ancestral territorial and non-marine state to the derived non-territorial and marine state was through a non-territorial and non-marine intermediate state. Dubois *et al.*(1998) did a comparative analysis of the association between mate fidelity and coloniality in waterbirds (wading birds and seabirds). They showed that the transition from a high to a low degree of coloniality occurred before the transition to higher mate fidelity. Beauchamp (1999) used the phyolgenetic approach to examine the effect of an evolutionary transition to coloniality on several breeding traits in birds. He selected 29 pairs of congeners, which included one colonial and one solitary breeding species. He found that coloniality appeared to be a weak force in the sexual diversification of body mass and plumage characteristics in birds. The results support the hypothesis that coloniality is associated with greater foraging efficiency, which allows colonial birds to increase parental effort. Recently, Varela *et al.*(2007) used the phylogenetic approach to study the effect of coloniality on predation. They analysed all 30 families of the Ciconiiformesas this order shows the highest prevalence of colonial breeding, with 77% of families exhibiting coloniality. The mapping of coloniality and nest vulnerability to predation on the phylogenies revealed numerous transitions. They suggested that the colonial/vulnerable state is especially exposed to predation as coloniality may often attract predators rather than provide safety.

Cost and Benefit Approach

Coloniality has its own costs and benefits as a consequence of the close proximity to conspecifics in densely distributed territories. A traditional approach has been to study coloniality in terms of trade-offs between advantages and disadvantages of nesting in groups. Thus, whenever it is beneficial, i.e. the overall balance is in favour of colonial breeding, it will be selected for; when there are more disadvantages than advantages, some other type of breeding system will be used (Brown & Brown 2001). Alexander (1974) first delineated the most likely costs and benefits of group living. He said that the costs of group living are more automatic and universal than its benefits. The necessary costs were (1) increased intraspecific competition for resources (e.g., food, nest sites or materials, mates), (2) increased ectoparasite or disease transmission and (3) attraction of predators. The potential direct benefits could be decreased predation, increased foraging efficiency and resource localization or limitations due to which organisms form groups. Alexander suggested that group living only appears because one or some combination of these three general extrinsic causative factors at some point offsets the automatic detriments of group living above the fitness of solitary individuals(Alexander 1974).Hoogland and Sherman (1976) explored the costs and benefits of living in different sized groups in the highly social Bank Swallow. They found that increased competition, physical interference, misdirected parental care and transmission of ectoparasites are the major disadvantages of Bank Swallow coloniality. By considering the advantages, they concluded that shortages of suitable breeding sites or the social facilitation of foraging does not explain the evolution of coloniality in the case of the Bank Swallow. But decreased predation was found to be an important factor in maintaining Bank Swallow coloniality.

The benefits of coloniality can be the consequences of two types of factors: those that originally caused birds to form colonies (causative factors) and those that maintain coloniality once individuals have clustered. The implicit assumption has been that it is more important to identify causative factors. The original advantage of forming colonies may not itself be sufficient to maintain them in the face of the inevitable disadvantages. It may be the secondary benefits that keep the net fitness effect of coloniality positive (Brown & Brown 2001). Various models and hypotheses relating to resource

distribution and utilization in colonial birds have been proposed to explain these causative factors.

The Information Centre Hypothesis

This hypothesis was first proposed by Ward and Zahavi (1973) and it has stimulated a lot of work and debate regarding the transfer of information in colonial nesting birds. Ward and Zahaviproposed that both communal roosts and coloniality have evolved as an adaptation for efficient exploitation of patchily and unpredictably distributed food sources. According to the hypothesis, successful foragers return to the colony after locating and exploiting a food patch and communicate the information to other conspecifics. Thus the colony or communal roosting site works as an information centre by providing information on the location of food. So the unsuccessful foragers of the colony improve their foraging efficiency by following the successful conspecifics. The hypothesis also predicts that the larger the colony size, the greater the pool of information will be on the whereabouts of good feeding places. For transferring information, successful foragers perform characteristic aerial displays to advertise the location of food to the unsuccessful foragers(Ward & Zahavi 1973). Reduced predation has a secondary role, concluded Ward and Zahavi, in the evolution of coloniality compared with the enhancement in foraging efficiency through information centres. Predation only helps in shaping the colony by choice of inaccessible or otherwise safe sites, optimum dispersal and group vigilance.

Though this hypothesis remained viable for a long period, there is little empirical evidence to support it. There are a few studies on colonial birds showing results in favour of the information centre hypothesis, for example, the Red-billed Quelea,*Quelea quelea* (Ward & Zahavi 1973), Cattle Egret, *Ardeola ibis* (Siegfried 1972), White Wagtail, *Motacillla alba* (Zahavi 1971), Cliff Swallow, *Petrochelidon pyrrhonota* (Brown 1988), Osprey, *Pandion haliaetus*(Greene 1987), Common Tern, *Sterna hirundo* (Waltz 1987) and Yellow-headed Blackbird, *Xanthocephalus xanthocephalus* (Brown & Brown 2001) . But various aspects of all these studies have been debated (Richner & Heeb 1996). There is no supportive evidence for information exchange in mixed species colonies so far. Moreover, Bayer (1982) showed that many observations regarded as evidence for information centres (e.g. synchronised departures and arrivals at the colony) were inconclusive and can be interpreted in other ways also. Richner and Heeb (1996) argued that there is no any logical answer why a successful forager should travel back to the colony or roost as the hypotheses predicts and thereby pay the time and energy cost of travelling (as reciprocal altruism is also unlikely in colonies). According to the hypothesis, the information about the location of unpredictable and patchy food sources is exchanged at the colony itself. So if only the unsuccessful foragers come back to the colony, the colony will hold the unsuccessful foragers only and there will be no one for them to follow later on. A recent study also finds that colonies have high mobility of individuals and this also limits the potential for this type of co-operation (Houston 1993). This also reduces the probability that a colony or roost can serve as an information centre. This assumption is also controversial asa food source can be stable for a limited time period only (e.g., a week or a month) in some location. But birds still continue aerial displays. This adds the cost of displaying, and there is no obvious compensating benefit for it. So this hypothesis lacks both a sound theoretical basis (Richner & Heeb 1996)and empirical support (Mock *et al.* 1988).

The Recruitment Centre Hypothesis

As an alternative to the information centre hypothesis, Richner and Heeb (1996) proposed that the benefits derived from group foraging, rather than from information transfer at the breeding colony, are more likely to be an evolutionary force for coloniality. According to this hypothesis, roosts and breeding colonies can serve as recruitment centres where the successful foragers can recruit other foragers to join them at a newly discovered food patch. Thus the benefits derived from group foraging may compensate for the cost of travelling back to the colony and revealing information about the food source. This hypothesis predicts that the aerial displays and calls at a roost or breeding colony serve ashonestsignals to communicate and recruit foragers. Richner and Heeb also suggested that successful foragers will return to the colony once a food patch has been discovered only when

$$BG + CR > BS$$

The total of the net benefit of group foraging (BG) and the time and energy cost of the return trip (CR) is higher than the benefit of staying at the patch and foraging singly (BS). There are virtually no empirical data supporting this hypothesis as most of the research work has been oriented towards the information centre hypothesis so far (Richner and Heeb1996). However, some colonial birds, e.g. Black Billed gulls (*Chroicocephalus bulleri*), Ring Billed gulls (*Larus delawarensis*), Cliff swallows (*Petrochelidon pyrrhonota*) have characteristic calls that can be considered as recruitment calls also (Brown & Brown 2001). One positive side of this hypothesis is that it does not require group selection. It is based on the costs and benefits of each individual of the colony. Moreover, it can also justify the origin of coloniality in the absence of other potential benefits (Brown & Brown 2001).

Commodity Selection Hypothesis

Most recently, Danchin and Wagner (2000) proposed that colonial nesting has evolved as a by-product of many individuals selecting commodities such as habitats and mates by imitating the choices of successful conspecifics. So it

may not be necessary for individuals to get direct benefits from nesting in colonies (Danchin & Wagner 1997).For example, animals might prospect potential breeding habitats and choose to breed in favourable environments (Wagner *et al.* 2000). Such a scenario could indirectly result in colonial breeding. Many empirical investigations of this hypothesis have appeared recently, e.g. on the Black-legged kittiwake, *Rissa tridactyla* (Suryan & Irons 2001), Gull-billed tern *Sterna nilotica*(Erwin 1978),Collared flycatcher, *Ficedula albicollis* (Doligez*et al.* 1999) and Great cormorant, *Phalacrocorax carbosinensis* (Schjorring*et al.* 1999), where it was regarded that reproductive success and potential partner quality as important conspecific cues for breeding colony selection. However, the role of current reproductive success on individual fitness could vary greatly between species with different life histories. So testing the hypothesis of commodity selection requires identification of the cues for each species and, probably, population (Tella *et al.* 1998). Koshciuch and Langerhans (2004) have suggested that the variability in reproductive success may be more accurate as a proximate cue for commodity selection compared with the mean reproductive success.

Hypotheses based on the cost–benefit approach have one pitfall in common that the costs and benefits of coloniality are

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