

Choice of Colony Size in Birds

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Most populations of colonial birds exhibit extensive variation in colony size. Field studies over the last decade have shown that individual birds breeding in colonies of certain sizes are apparently more successful than those settling in colonies of other sizes, yet size variation persists. Enough information is now available to suggest four explanations for how birds choose colonies and why colonies vary in size.

Coloniality is a pervasive form of social organization in some taxa of birds, being most common in waterbirds. The evolution of this spacing pattern has attracted considerable attention and debate^{1,2}. The predominant approach in field studies has been to measure the presumed social costs and benefits of coloniality as a function of group size¹, using the natural variation in colony size that occurs within many populations³⁻⁸. Virtually all groups of colonial birds contain species in which extensive variation in colony size within populations has been observed (Table 1). Many of these species at times also breed solitarily.

Surprisingly, why colonies vary in size is unknown for most species, mostly because little if any research has addressed explicitly how birds choose colony size. Colony size variation within a population is especially perplexing given that several studies³⁻⁸ have demonstrated that individuals living in colonies of a given size appear to be less successful than those in other colony sizes, but the less-successful colonies still persist. Any general theory for the evolution of coloniality, if such a theory is possible^{1,2}, must account for colony size variation and for the choices individuals make that lead to this variation.

Recent field studies suggest at least four potential explanations of the observed colony size variation within a species: (1) individuals sort themselves among colonies in an ideal free distribution⁹, with colony

size reflecting the relative quality of the habitat in which each colony is located; (2) social costs and benefits of grouping lead to certain colony sizes being optimal for a given individual, and individuals have different colony size optima; (3) energetic, temporal or social constraints reduce an individual's ability to gather sufficient, or reliable enough, information to make optimal choices of colony size; and (4) colony size variation may reflect a 'despotic distribution'⁹ of birds, with some individuals forcing other individuals into inferior sites. These explanations are not mutually exclusive, and more than one may apply in most species.

Fitness consequences of colony size

Consideration of colony choice requires first knowing something about an individual's expectation of success in colonies of different sizes. There are now data from which it is possible to estimate, for some species at least, the fitness consequences of choosing colonies of different sizes. Based on patterns of how observed costs and benefits of group living change with colony size, one can predict which colony size will result in the highest average reproductive success for individuals, and thus which colony size should be preferred (Box 1). There are four general patterns: fitness can either increase, decrease, or remain constant with colony size, or an intermediate size range can be favored (Box 2).

Do individuals prefer to settle in the colony size where their average expectation of success is greatest? In some species, individuals do seem to prefer colonies of particular sizes even when all possible choices are presumably available (Fig. 1); yet even in these species, sizeable fractions of the population still settle in the other, less-popular colony sizes. Other populations of the same species may exhibit little observable colony size preference (Fig. 1).

Ideal free distribution of colony sizes

The ideal free distribution model of habitat selection⁹ predicts that all

individuals, who are of equal competitive abilities, move among the available sites and settle in densities such that rewards for all individuals are equal. Although empirical support for such a model in general is equivocal¹⁰, bird colonies at first glance might seem to be likely candidates for ideal free processes.

In some colonial birds, colony size may reflect the amount of suitable foraging habitat present within each individual's maximum foraging range¹¹. A positive correlation between amount of foraging habitat and colony size has been demonstrated¹¹. When individuals from a colony share their foraging habitat with individuals from neighboring colonies, colony size declines, presumably due to competition and thus 'loss' of some potential foraging habitat¹². In contrast, an experimental study that examined potential differences among colonies in local food abundance found no evidence for resource differences among colonies of different sizes⁸.

If colony size is adjusted to local food abundance or other habitat features, the observed colony size distribution could be ideal free, but only if individuals in different colonies received the same pay-offs. All else being equal, individuals could move between sites until they distributed themselves such that harvest rates (or other types of gain) were the same for each individual.

In most colonies, however, all else is not equal. Once they have formed a colony of a given size, individuals can expect additional costs and benefits that stem directly from a variety of social effects that are determined largely by the number of conspecifics present¹. Thus, even if colonies formed initially due to ideal free processes, individuals in different-sized groups cannot necessarily expect the same fitness. This is illustrated well in herons, in which colony size may be influenced strongly by the amount of food available locally, yet individuals in large colonies have a higher average annual reproductive success that can most likely be attributed to social effects such as enhanced predator avoidance and information transfer¹¹. We therefore are still left with the problem of why

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Table 1. Examples of colony size variation selected from the major taxonomic groups of colonial birds

Species	Range in colony size (no. of nests)		Ref.
	Minimum	Maximum	
Fulmar, <i>Fulmarus glacialis</i>	1	>100 000	38
Gannet, <i>Sula bassana</i>	17	59 000	39
Adelie penguin, <i>Pygoscelis adeliae</i>	<10	>1200	40
Gentoo penguin, <i>P. papua</i>	2	271	32
Frigatebird, <i>Fregata</i> sp.	1	600	41
Olivaceous cormorant, <i>Phalacrocorax olivaceous</i>	≤25	2000	42,43
Louisiana heron, <i>Hydranassa tricolor</i>	≤25	9666	42,43
Cattle egret, <i>Bubulcus ibis</i>	≤25	6000	42,43
White ibis, <i>Eudocimus albus</i>	≤25	30 000	42,43
Common eider, <i>Somateria mollissima</i>	1	1623	44
Lesser kestrel, <i>Falco naumanni</i>	15	100	45
Eleonora's falcon, <i>F. eleonora</i>	2	256	46
Osprey, <i>Pandion haliaetus</i>	1	306	47
Black-headed gull, <i>Larus ridibundus</i>	1	1500	48
Mew gull, <i>L. canus</i>	1	500	48
Ring-billed gull, <i>L. delawarensis</i>	20	80 000	49
Laughing gull, <i>L. atricilla</i>	≤25	17 326	42,43
Little tern, <i>Sterna albifrons</i>	1	46	48
Common tern, <i>S. hirundo</i>	1	140	48
Sandwich tern, <i>S. sandvicensis</i>	4	1150	23
	≤25	20 367	42,43
Royal tern, <i>Thalasseus maximus</i>	≤25	7210	42,43
Dovekie, <i>Alle alle</i>	≤20	500 000	51
Thick-billed murre, <i>Uria lomvia</i>	10	800 000	51
Atlantic puffin, <i>Fratercula arctica</i>	10	148 000	51
Cassin's auklet, <i>Ptychoramphus aleuticus</i>	≤25	>50 000	42
Passenger pigeon, <i>Columba migratorius</i>	1	>1 000 000	52
White-fronted bee-eater, <i>Merops bullockoides</i>	10	250	53
Blue-throated bee-eater, <i>M. viridis</i>	1	450	53
Carmine bee-eater, <i>M. nubicus</i>	15	5000	53
Bank swallow, <i>Riparia riparia</i>	2	451	3
	12	>1000	54
	1	390	16
Cliff swallow, <i>Hirundo pyrrhonota</i>	1	3500	8
Fieldfare, <i>Turdus pilaris</i>	1	20	30
Yellow-rumped cacique, <i>Cacicus cela</i>	2	100	4
Brewer's blackbird, <i>Euphages cyanocephalus</i>	5	30	55
Tricolored blackbird, <i>Agelaius tricolor</i>	50	100 000	31

some individuals choose to nest in small colonies, where they are likely to be less successful on average.

Since the costs of parasite/pathogen transmission and increased social competition are probably universal for animal aggregations¹³, these costs in general are likely to change any fitness pay-offs that might initially be influenced by environmental characteristics of different colony sites. For example, a recent attempt to explain the evolution of coloniality in barn swallows (*Hirundo rustica*) is apparently based on the ideal free distribution¹⁴, but ideal free processes are unlikely in this particular case because individuals in different-sized colonies differ markedly in their expected annual reproductive success, due mostly to increased ectoparasitism in larger colonies⁷. The ideal free distribution can probably most easily explain colony size variation in species in which colonies do not have important group-size-dependent social costs or benefits associated with them, or in which the social costs and benefits reach an asymptote above a given colony size.

Differences among individuals in optimal colony size

The observed colony size variation may reflect alternative optimal sizes for different individual birds, depending on individual status, age or quality^{15,16}. Not all individuals necessarily have the same expectation of success in a given group or habitat, and they should sort themselves to maximize their own expected fitness¹⁰.

A game-theory approach has been applied to predict when animals should shift between different foraging groups^{10,15}, and these ideas may apply to colonies. For example, younger seabirds breeding for the first time have poor success in competing for nesting space with older birds within a colony, and often lose some of their offspring to cannibalistic attacks by older colony residents¹. Perhaps as a response, many first-time breeders settle in separate, smaller colonies¹⁷, where their reproductive success can be as high as in colonies of older birds¹⁸. Similarly, in a species in which foraging information transfer within colonies is important^{8,19}, some evi-

dence now suggests that certain individuals who appear to be particularly adept foragers may avoid large colonies and their attendant costs altogether, instead settling in extremely small colonies (C. Brown, unpublished data).

Asymmetries among individuals within a colony may change the expected pay-offs of colonies of a given size. As a result of age, sex or other factors, individuals may differ in their ability to withstand the ectoparasites²⁰ often prevalent in colonies, to compete for the safer nest sites²¹, to forage efficiently, or to avoid predators.

For example, an individual's spatial position within a colony may have a huge influence on its expectation of success²¹. Individuals nesting on the edge of a colony typically experience reduced nesting success, which is most often attributed to increased predation¹. An individual faced with the choice of joining

an existing large colony and nesting in a vulnerable site at the periphery, or settling in a smaller colony, may in fact do as well or better by choosing the smaller site. This should be especially true if the existing large colonies are already sufficiently large that predators are likely to be attracted²², which would increase the likelihood of an edge nest being attacked (while perhaps simultaneously decreasing the likelihood of a center nest being attacked, through enhanced predator mobbing⁴ or satiation¹). As a result, recruitment may stop at larger colonies, and new arrivals may shift to smaller colonies.

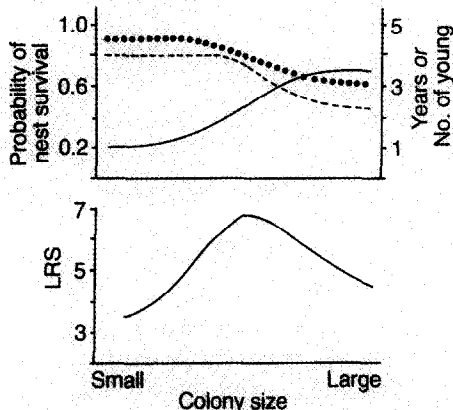
Constraints on ability to gather information

If a theoretical optimal colony size exists for a given individual, or if an individual seeks only to settle in the smallest or largest colony available, the individual may nevertheless have difficulty locating and

Box 1. Optimal colony size

The optimal colony size is defined as the one in which average lifetime reproductive success (LRS) is highest. At present there are no studies in which LRS for birds in different-sized colonies is known, although LRS has been calculated for a communal species that breeds in different-sized social groups²⁹. LRS can be estimated by measuring its two major components: expected lifespan and annual reproductive output. By determining average annual survival of adults and their reproductive success in colonies of different sizes, expected LRS (lifespan times number of offspring per year) can be calculated for each colony size²⁹. To understand better how the costs and benefits of coloniality interact in different colony sizes, annual reproductive success can in turn be broken down into its components.

For example, the figure below shows a hypothetical case in which the probability of a nest surviving to produce fledglings (dotted line) decreases with colony size due to infestations of deleterious ectoparasites^{5,7}; the number of chicks per successful nest (dashed line) decreases with colony size due to increased competition for food and nestling starvation²⁰; and average survivorship of adult breeders (solid line) increases with colony size due to enhanced foraging efficiency through information transfer⁸. When these three variables are multiplied together, the resulting LRS is highest for individuals in intermediate-sized colonies, a result not readily apparent when each component is examined separately.



settling in a colony of that size. How might individuals gain information on colony size?

Birds that arrive after colonies have become active may simply assess the number of existing active nests. Individuals may have more difficulty predicting the size of a colony early in the nesting season, before or as colony sites are occupied by residents. A mechanism that early-arriving birds may use is synchronous flocking. Many colonial birds exhibit conspicuous swarming behavior early in the breeding season, most often during the time of colony establishment^{23,24}. Large flocks arrive synchronously at potential sites, remain briefly, depart, and sometimes

move to another colony. Swarming tends to be less prevalent in later-arriving birds²³. This behavior is not understood, but swarming may in fact be used by group members to predict the likely size of a potential colony site by assessing the number of birds interested in it. Other, also potentially unreliable, cues that early arrivals might use to predict eventual colony size include assessing the number of old nests remaining from previous years¹⁴ (if the species builds long-lasting nests) or gauging the size of the environmental patch available to the colony (e.g. size of island or nesting tree).

Choice of colony size is also affected by how large an area and how many potential colonies an individual can visit before deciding on a site. Without relatively comprehensive information on what colony sizes are potentially available in a local area, an individual may not be able to make its best choice; this is the same problem that a foraging animal has in allocating time to sampling the environment before choosing a patch or a particular type of prey²⁵. Over how large an area does an individual sample before deciding on a colony?

Data are lacking on individual search areas of birds seeking colonies. Time of year may have a large impact on the degree to which an individual can visit a range of potential colonies before choosing one. In seabirds, early nesters may spend several weeks visiting different sites before finally settling, whereas late nesters move into sites and begin breeding much more rapidly, and presumably after spending less time visiting other colonies²⁶. If late nesters are regularly constrained by a shortened breeding season, they may not be able to be as choosy in selecting sites. Even for those individuals who can afford the time to assess several different colonies, potential limitations on the degree to which they can learn and later recall the associated features of each site may prevent them from making the best choice among the colony size options available. That the wrong choices are sometimes made is suggested by instances in which all nests in a colony are abandoned and the site deserted, perhaps due to local food shortages caused by resource depletion¹.

Individuals are not assured of reliable information on colony size even if they have the time and cognitive abilities to assess and remember all available colony sites and choose among several of these colonies. For example, they may assess accurately the size of a colony at the time they settle there, but a colony can subsequently increase or decrease after an individual has begun nesting. In gulls, some pairs may leave the colony site altogether or others may move toward the colony's center, leaving some pairs nesting as isolates or in small sub-colonies that are much smaller than the colony they originally chose^{24,26}. Perhaps more frequently, later waves of incoming birds arrive, markedly increasing a colony's size^{16,26}. Swallow colonies may increase by up to an order of magnitude after the first residents have settled¹⁶.

Thus, a potential disadvantage of early nesting is that the colony chosen may shift unpredictably in size, and once an individual begins nest construction or egg laying its prior investment in time at that site may preclude it from leaving and searching elsewhere, regardless of how its colony's size changes. Some colonial birds may delay breeding at a site until the number of birds there stabilizes²⁴, which may be one way of avoiding getting stuck in a colony of an undesirable size. Late nesting in general is regarded as disadvantageous, but birds nesting late may have a more predictable colony size set to choose from (if they have the time to assess what is available), and thus potentially may come closer to selecting the colony size that is best for them.

Colonies as despotic distributions

So far we have assumed that individuals have at least some freedom to make active choice of colony sites. In some species, however, social dominance hierarchies or other asymmetries in competitive abilities among individuals may enable certain individuals to exclude others from nesting at a given site. In these cases the excluded individuals may have to settle for inferior colonies, meaning that they may have little real 'choice' in where to nest. The resulting variation in colony size may represent a despotic

distribution⁹ in which dominant individuals live in a colony that is the best size for them, keeping it at that size by preventing others from settling.

Colonies resulting from despotic interactions are most likely in polygamous colonial species with social dominance relationships. The best evidence for this type of colony settlement comes from polygynous yellow-rumped caciques in which the aggressive, more dominant females exclude other females from particular sites and thereby regulate colony size²¹. Females excluded from the favored sites settle in other colonies or as solitaries, where they are more likely to suffer predation upon their nests⁴.

Other constraints on making colony size choices

Physical restrictions on the available nesting substrate within colonies may force birds into smaller colonies than they would otherwise prefer. This may be especially important in those species in which fitness apparently increases roughly linearly with colony size (Box 2); there may be few sites that can physically support a colony that increases indefinitely. In these cases some individuals would have to accept smaller, less favorable sites (or not breed at all). Similarly, limitations in the total number of suitable sites⁴ may constrain an individual's choice. Caciques seem to prefer to nest in small colonies or solitarily to minimize competition for food, but the lack of sufficient numbers of predator-free nest sites forces these birds into larger colonies than they apparently prefer¹.

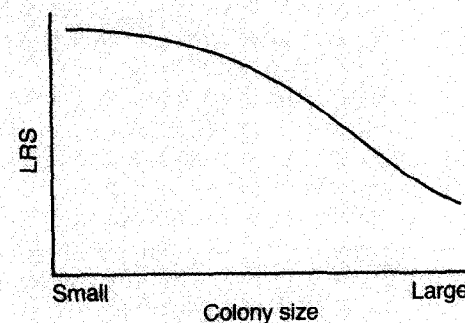
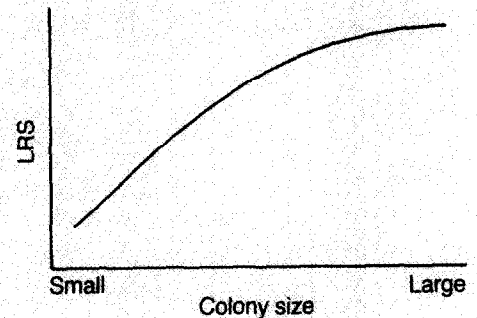
Some colonial birds, especially seabirds, show marked fidelity to colonies, and in some cases to nests, used during the previous year²⁷. Individuals thus may return repeatedly to breed at the same colony site year after year, occasionally even when unsuccessful there in the past²⁷. The advantages of site fidelity in colonial birds, most of which maintain only small, nest-centered territories, are not clear; presumably these advantages center around experience in avoiding predators and finding food near a colony where one has lived previously²⁸.

Whatever the benefits of site

Box 2. Colony size and reproductive success

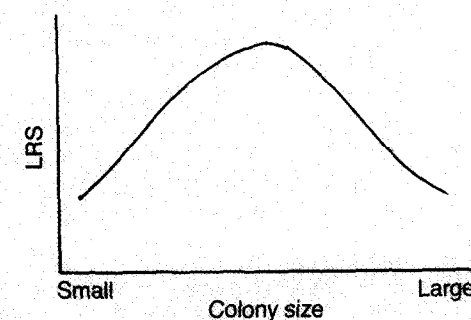
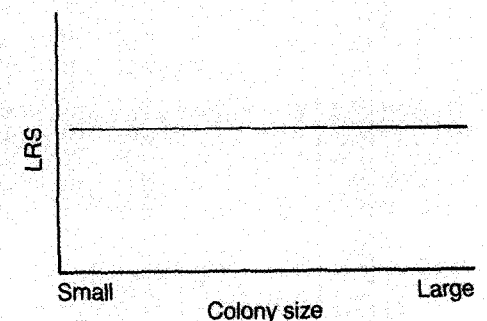
Determining the optimal colony size within a population requires data on how average survivorship of adult breeders and annual reproductive success change with colony size (see Box 1). The types of simple optima curve that are possible are shown in the figures below. No studies have examined systematically the effects of colony size on adult survivorship, but there is some information on how annual reproductive success varies with colony size.

Large colonies favored: An increase in annual reproductive success with colony size or nest density has been reported in a number of species, from seabirds to passerines¹. This increase is usually attributed to enhanced predator avoidance by birds in larger groups. Occasionally, large colonies do better because small colonies form near poor or unstable food sources that are likely to fail³¹, or because small colonies consist of less-experienced, younger birds³².



Small colonies favored: Several studies have shown that reproductive success is lowest in larger colonies, due to high ectoparasite loads⁷, increased interference from conspecific neighbors in the form of cannibalism¹ or increased risk of predation²², presumably because larger colonies are more conspicuous and attractive to predators.

No size favored: Annual reproductive success does not always vary with colony size^{3,33,34} or nest density³⁵. This pattern may be the result of trade-offs between costs and benefits. In cliff swallows, for example, annual reproductive success reflects the benefits of transfer of foraging information and the costs of ectoparasitism, both of which increase with colony size⁸ and directly affect the nestlings' prospects of fledging.



Intermediate size favored: High predation rates in small colonies of fieldfares and increased starvation rates in large colonies result in annual reproductive success being highest in intermediate-sized colonies³⁰. In herring gulls (*Larus argentatus*), reproductive success is highest at intermediate nest densities, probably because of increased cannibalism at high densities and the presence of inexperienced, inferior breeders at low densities³⁶. Intermediate colony sizes also may be favored in mew gulls and sandwich terns, in which solitary nests are less likely to survive than colonial nests, but among those in the colonial category, nests in the smaller or medium-sized colonies seem to have higher success^{23,37}.

fidelity, its consequence is that colonial individuals may be less likely to leave a site used in the past, regardless of how that colony's size in the present year may change

through the addition or subtraction of other residents. The benefit of experience at that site may outweigh the costs of living there even when the colony is of a less-

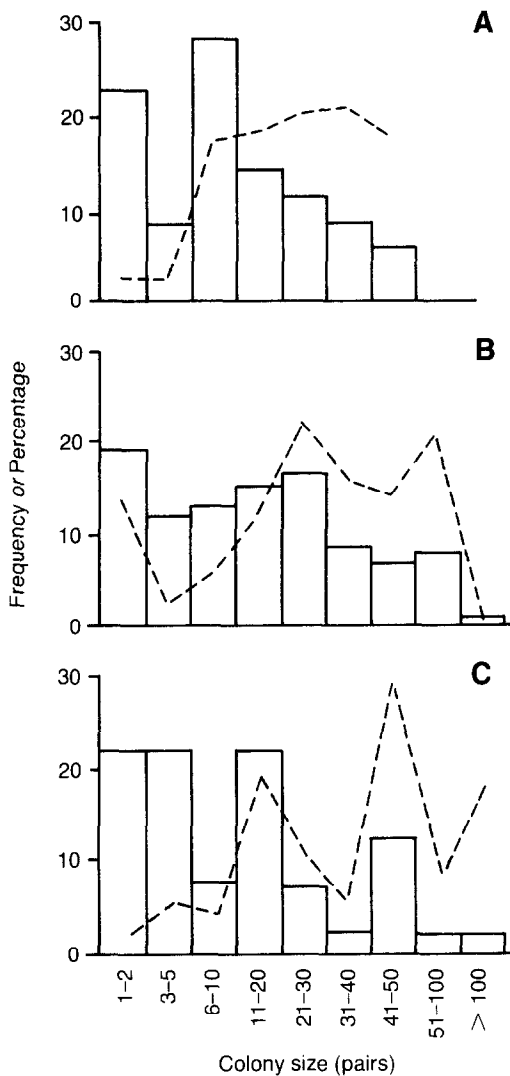


Fig. 1. Frequency distributions for colonies of different size classes (bars) and percentage of pairs breeding in each size class (dashed lines) for three populations (A, B, C) of common terns nesting along the Vistula River, Poland. Redrawn from Ref. 48 with permission.

favorable size. This point illustrates especially the importance of knowing the histories of individuals that comprise a given colony, for interpretations of both why colonies vary in size and why certain birds breed in colonies of different sizes.

Unanswered questions

This review has outlined several factors that may generate and maintain variation in colony size. Our understanding of the cues that individuals use to choose colonies of different sizes is still rudimentary. Progress will be made by focusing on known individuals, preferably of different ages, status and quality, and compiling their histories during the period of initial colony assessment and establishment. How many different sites did they visit, and what were the sizes of these colonies at the time they settled (i.e. what options were available to them)? Do long-lived individuals always select

colonies of the same size? How does individual condition affect the choices made, and are there really different colony sizes that are optimal for different individuals within a population? To what degree do individuals incur fitness reduction by either selecting a colony of suboptimal size or being forced into a colony of suboptimal size by subsequent activities of other birds? How synchronous are the arrivals at a colony, and how predictable is the final colony size at the time of settlement for breeders at different times of the year?

We still lack a general theory of colony choice. Such a theory will probably consist of at least five major parts: the ideal free distribution in a broad sense; the extensive body of documented social costs and benefits of group size; consideration of the competitive asymmetries among individuals within a group; theories of patch choice and sampling, developed to date mostly for foraging animals; and the concept of risk sensitivity. This review has touched on all of these aspects except the latter. That animals may be sensitive to their expected probabilities of surviving or reproducing has led to advances in foraging theory²⁵. If animals make foraging decisions based on these expectations (for example, whether to forage socially or solitarily), it seems equally possible that they could choose colony sizes in the same way. Does colony size affect the observed variance in reproductive success independent of the mean? Existing data on colonial birds have not been analysed with this question in mind, but if the answer is yes, risk must be incorporated into models of colony choice. Avian coloniality clearly provides many opportunities for further empirical and theoretical progress.

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Avian Cooperative Breeding: Old Hypotheses and New Directions

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In cooperatively breeding birds, individuals that appear capable of reproducing on their own may instead assist others with their breeding efforts. Research into avian cooperative breeding has attempted to reconcile the apparent altruism of this behaviour with maximization of inclusive fitness. Most explanations of cooperative breeding have suggested that philopatry is enforced by ecological constraints, such as a shortage of resources critical to breeding. Non-dispersers may then benefit both directly and indirectly from contributing at the nest. Recent research has shown that such benefits may be sufficient to promote philopatry, without the need for ecological constraints, and emphasizes that consideration of both costs and benefits of philopatry is essential for a comprehensive approach to the problem. The growing body of data from long-term studies of different species should combine with an improved phylogenetic perspective on cooperative breeding, to provide a useful base for future comparative analyses and experimentation.

The apparent altruism exhibited by cooperating birds has stimulated three decades of intense theoretical and empirical research, recently culminating in a number of monographic reports of single-species studies¹⁻³ and a synthetic review⁴. These and many other reports have tended to emphasize the similarities between cooperative breeding systems, and in particular the role of ecological constraints'. Philopatry by birds that should be capable of reproducing independently is believed to occur because key resources for breeding, such as mates or territories, are limited due to

competition. A corollary of this view is that once philopatry has been explained, helping behaviour is likely to emerge for any of a series of reasons, including the need to gain breeding experience⁵, the benefits that arise from aiding close relatives⁶, the need to pay rent⁷, and most recently, the suggestion that birds help merely because they receive the appropriate stimulus (begging young)⁸.

Emlen⁷ was able to claim that 'this hypothesis, that habitat saturation provides the primary impetus for philopatry . . . has become the modus operandi for ecological thinking concerning the evolution of helping behavior'. More recently, Stacey and Ligon⁹ have suggested that the constraints on successful dispersal as a source of philopatry have been overemphasized⁹. Such emphasis on costs to dispersal has led to an artificial separation of the questions 'Why stay at home rather than disperse?' and 'Why help once at home?' Because some of the benefits of helping are also benefits of philopatry, the distinction is often blurred. In addition, the recent application of biochemical techniques to avian systematics has revealed that philopatry and cooperative breeding may have historical origins within certain taxa. In this review, we evaluate the costs, benefits and phylogenetic basis of philopatry, with particular emphasis on research that has been reported since Brown's compilation⁴.

Problems with habitat saturation

Many cooperative breeders are territorial, and long-term studies of North American species have strongly promoted the hypothesis that 'saturation' of habitat with established territories limits the availability of breeding space to novices¹⁻³. However, three separate lines of reasoning raise doubts about the universality of this model.

First, assuming space for breeding is the critical resource, several recent studies of territorial cooperative breeders demonstrate that helpers may stay in their natal territory even when vacant territories are available⁹⁻¹¹. Second, an important feature of the habitat saturation model is its emphasis that ecological constraints impose philopatry. Clearly, most avian species are ecologically constrained, yet only a very small proportion (3%) are known to exhibit this form of sociality (although since the social systems of most tropical species are poorly documented, this proportion could be higher). In many species, young birds form 'floating' non-territorial subpopulations, illustrating that saturated habitat does not necessarily force nonbreeders to remain at home⁹.

A final problem is that many cooperative breeders have probably been studied in preferred habitat, where adult mortality is low, and production of young exceeds mortality of breeders⁹. Thus, habitat saturation may be interpreted as a

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