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## CHAPTER 7

REPRODUCTIVE ENERGY EXPENDITURE, INTRASPECIFIC VARIATION  
AND FITNESS IN BIRDS

TONY D. WILLIAMS AND FRANÇOIS VÉZINA

1. Introduction .....	355
1.1. Intraspecific (Interindividual) Variation .....	356
1.2. Doubly-Labeled Water and Other Methods for Measuring Energy Expenditure .....	358
1.3. Aims, Objectives, and Limits .....	360
2. Is Reproduction Energetically Costly, and at What Stage Is It Most Costly? .....	360
3. Intraspecific Variation in Daily Energy Expenditure: Biological Variation or Measurement Error? .....	363
3.1. Measurement Error .....	363
3.2. Handling or Treatment Effects .....	371
3.3. Individual Variation in DEE from Field Studies Relative to Measurement Error .....	372
4. Repeatability of Daily Energy Expenditure Measurements	374
5. Individual, Environmental, and Activity-Related Correlates of DEE .....	378
5.1. Individual Attributes .....	379
5.2. Environmental Factors .....	380
5.3. Activity-Related Variation .....	382
5.4. Summary .....	382
6. Metabolic Rate and Body Mass: Intraspecific versus Interspecific Scaling .....	383
6.1. Intraspecific Variation in Body Composition and Metabolic Rate .....	385
7. Relationships between DEE and Measures of Reproductive Effort or Fitness .....	386
7.1. Timing of Laying, Egg Size, and Clutch Size .....	390
7.2. Offspring Growth and Quality .....	391
7.3. Brood Size and Provisioning Rate .....	391
7.4. Costs of Reproduction: Survival and Future Fecundity	392
7.5. Summary .....	393
8. Conclusions and Recommendations for Future Research ...	396
References .....	399

INDEX .....	407
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## CHAPTER 1

## AVIAN COLONIALITY

## Progress and Problems

CHARLES R. BROWN  
and MARY BOMBERGER BROWN

## 1. INTRODUCTION

Avian social systems during the breeding season can be classified into three major types: territorial, cooperative or communal, and colonial. This classification is based on the degree of conspecific association in use of space, and some species may exhibit more than one type within or between populations. Coloniality in birds is typically defined as the breeding by a number of individuals at a more or less centralized place from which colony residents regularly depart for search for food (Siegel-Causey and Kharitonov, 1990; Wittenberger and Hunt, 1985). Colonial nesting is the least understood of all avian breeding systems; it is even difficult to define what constitutes a colony for some species. What causes sometimes thousands of mostly unrelated individuals to nest in a single, spatially restricted site where the penalties of close crowding can often diminish reproductive success? Why do colonies of the same species within the same population often vary by several orders of

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essentially solitary nesting and others nesting in closely spaced territories. Most of the work we review here was done on obviously colonial species such as kittiwakes or swallows that nest in locally high densities, often packed into a small, restricted space, and feed in non-defended areas away from the nest. But other species such as ducks, some herons and gulls, and blackbirds may defend small feeding territories and still interact closely with dozens of neighboring conspecifics during the mobbing of predators and in other contexts. For the purpose of this review, we regard a species as colonial if it clusters its nests enough to have measurable interactions with neighboring conspecifics while at the same time not defending feeding territories around the nest. One way to designate a group of nesting birds as a colony in the field is to see whether they respond simultaneously to the approach of a predator or depart from their nests simultaneously to forage (Brown and Brown, 1996).

## 2. HISTORICAL BACKGROUND

Speculation as to the causes of animal coloniality began as early as the fourth century B.C. with Aristotle's *Historia Animalium* (Thompson, 1910). It continued with Allee (1951, 1938, 1931) and Darling (1938). Darling argued that colonial nesting socially stimulated birds and allowed them to synchronize their reproductive activities, and consequently, they had greater nesting success. His emphasis on the importance of reproductive synchrony has been embraced by many current studies that have sought to measure how fitness varies with synchrony (see Section 5.3.3); in addition, others have emphasized how correlates of fitness such as extra-pair mating may vary with breeding synchrony (Kempenaers, 1997; Weatherhead, 1997; Stutchbury and Morton, 1995). Although "social stimulation" was discredited as anything more than a proximate consequence of coloniality (Orians, 1961), Darling's (1938) suggestion that birds were more successful in large colonies because they were more synchronous there was essentially the first serious attempt to explain why birds nested in colonies.

That the social system of a species was often related to the distribution of its food or nesting sites and type of predation it experienced was first hypothesized by Lack (1966, 1954) and studied in some detail by Crook (1965, 1964). In particular, Crook's (1964) comparative analysis of social systems in African weavers was the first to examine a single group with different breeding systems and see how these differences related to ecology. Although not addressing explicitly the adaptive significance of

magnitude in size? These deceptively simple questions have frustrated ornithologists for decades.

The study of coloniality is important to other aspects of avian biology. For example, many of the costs and benefits of colonial nesting apply to all social animals, and thus understanding them in colonial species may aid us in analyzing the evolution of cooperative or communal breeding systems, most of which also involve groups of various sizes. The factors that cause colonies to form and vary in size may operate similarly with foraging groups or leks, and thus coloniality may have much to tell us about the evolution of grouping more generally. There are epidemiological parallels between bird colonies and human cities, and understanding parasite or pathogen transmission dynamics within or between colonies may provide clues to similar processes with humans or other animals (Grenfell and Harwood, 1997). In general, coloniality, with animals occupying discrete habitat patches of different characteristics, provides a natural framework to investigate metapopulation biology (Hanski and Gilpin, 1991), source-sink dynamics (Puliam, 1988), and population-genetic structure.

Unlike with territoriality, which can be explained in terms of economic defensibility (Wittenberger, 1981; Brown, 1964), or cooperative breeding, which can be understood in terms of inclusive fitness theory and habitat limitation (Emlen, 1994; Brown, 1987; Woolfenden and Fitzpatrick, 1984; Hamilton, 1964), work on coloniality (and communal roosting; Beauchamp, 1999b) has not uncovered general rules that can easily explain either its evolution or maintenance. Recent progress has been made, however, and one purpose of this review is to highlight advances that offer promising approaches and new insight into these old problems. We also critically evaluate some of the conventional wisdom about coloniality and offer suggestions for future work.

Coloniality is the second most common type of avian social organization after territoriality. Colonial nesting occurs in most avian groups (Rolland *et al.*, 1998; Brown *et al.*, 1990; Lack, 1968), being especially common in waterbirds. Lack's (1968) estimate that 13–14% of the world's birds are colonial is often quoted, although his definition of a "colonial" species is unknown. In a tabulation of 141 avian families, Crook (1965) reported coloniality occurred in 19%. Closer to 30% of species were classified as colonial in a sample that included representatives of most major ecological groups of birds (Rolland *et al.*, 1998). Part of the difficulty in knowing coloniality's prevalence among birds is defining a colony (Clarke and Fitz-Gerald, 1994; Buckley and Buckley, 1980b; Coulson and Dixon, 1979). In some species, individuals show varying degrees of conspecific association during breeding, with some

colonial nesting, Crook anticipated much of the later work on coloniality, noting that group feeding was associated with patchy, abundant food; that colonies afforded advantages associated with vigilance and mobbing of predators; that center nests within a colony were safer than peripheral ones; that colonies were often situated in sites inaccessible to predators; and that birds sometimes stole nesting material from nearby nests within a colony.

The first empirical studies of coloniality that had wide impact were those of Orians (1961) and Horn (1968) on blackbirds in North America and Kruuk (1964) and Patterson (1965) on Black-headed Gulls (*Larus ridibundus*) in Europe. Orians (1961) collected systematic data on nesting success in Tricolored Blackbird (*Agelaius tricolor*) colonies of different sizes, finding that smaller colonies were more likely to fail completely. Working on loosely colonial Brewer's Blackbirds (*Euphagus cyanocephalus*), Horn (1968) described cases of birds following each other from colony sites and suggested that coloniality facilitated such behavior. His observations foreshadowed the fascination with information centers that developed five years later with the appearance of Ward and Zahavi's (1973) information-center hypothesis (see Section 6.1). Horn's (1968) study is best known, however, for developing the "geometrical model" to explain coloniality. This model posits that travel-distance considerations can sometimes lead to clustered nesting (see Section 6). Kruuk (1964) experimentally measured predation rates and how colonial Black-headed Gulls responded to predators of different kinds. Patterson (1965) compared the success of solitary nests with that of colonial nests, and Patterson was also among the first to measure the effect of nest density within colonies. These gull studies suggested the potential importance of coloniality in helping birds avoid predation more effectively and helped to establish the conventional wisdom that antipredator benefits of colonial nesting are widespread.

Studies of coloniality got a boost in the early 1970s when Alexander (1974, 1971) summarized the three principal selective forces leading to social living as: (1) the need for individuals to aggregate where limited, critical resources (e.g., nesting sites) are found, and the ability for individuals in a group to (2) avoid predators better or (3) find food more easily. Alexander also pointed out that social animals probably experience two automatic costs of group living, that of increased parasite and disease transmission and increased competition for limited resources such as food or nesting sites. Although Alexander's ideas were not new and had been stated to various degrees by Allee (1951, 1938, 1931), Summers-Smith (1954), Crook (1964), Lack (1968, 1966, 1954), Lubin

(1974) and others, his review focused much of the subsequent study of coloniality.

The papers by Alexander (1974, 1971) also spawned one of the more influential empirical studies of avian coloniality. Using highly colonial Bank Swallows (*Riparia riparia*), Hoogland and Sherman (1976) used natural variation in colony size to test many of the potential social and ecological costs and benefits of group living. Their focus on comparing birds at different colony sites was a new approach to studying coloniality at that time. Simultaneously, Snapp (1976) conducted a similar study on Barn Swallows (*Hirundo rustica*), in which she also measured the effect of colony size on various breeding parameters. This early emphasis on swallows has continued to date, with this group figuring prominently in much of the key conceptual literature on coloniality.

To some degree, Hoogland and Sherman's (1976) and Snapp's (1976) success established a paradigm for research on coloniality, with dozens of subsequent field studies focusing on how putative costs or benefits changed with colony size—or between solitary versus colonial breeders—in various species (Brown and Brown, 1996; see Section 5). While yielding a large body of knowledge on how different costs and benefits vary with group size, this approach has not provided general answers to why birds form colonies. It also has not addressed the underlying causes of variation in group size among colonial species (see Section 9). Only recently have researchers begun to break away from the classical approach of measuring different costs and benefits and started to collect data or offer hypotheses to explain why colonies form and vary in size.

### 3. PHYLOGENETIC ANALYSES

Phylogenetic analyses use patterns of similarities and differences across taxa to make historical inferences about structure, function, and behavior. These analyses have proven useful in understanding some kinds of social behavior (Brooks and McLennan, 1991; Basolo, 1990). Although potentially limited by the accuracy and completeness of the phylogeny used, this approach is probably the best way to answer the historical questions of whether solitary or colonial breeding is the ancestral state in birds and how many times coloniality has evolved within the class. Multiple evolutionary appearances of coloniality would suggest that it is a direct consequence of particular ecological conditions

(e.g., food distribution, extent of predation), whereas few evolutionary appearances would suggest it is a phylogenetically constrained behavior that might have little relevance to a species' current ecology. Resolving these alternatives is important, because if the latter is the case, then measuring the fitness costs and benefits of coloniality in contemporary time might not necessarily reveal the original selective pressures that initiated this form of social organization.

Relatively few phylogenetic analyses of avian coloniality have been done. The first was by Siegel-Causey and Kharitonov (1990), who summarized the occurrence of colonial nesting across the major groups of birds. In the absence of a comprehensive phylogeny at the time their paper was written, they identified at least ten separate avian lineages in which coloniality had evolved. Siegel-Causey and Kharitonov (1990) concluded coloniality is a labile form of social behavior that has appeared independently many times among birds and is derived from solitary, territorial nesting.

Rolland *et al.* (1998) reached a similar conclusion when they did a formal phylogenetic analysis of coloniality using the molecular phylogeny of Sibley and Ahlquist (1990). Rolland *et al.* (1998) focused on three superorders (Apodimorphae, Strigimorphae, Passerimorphae) that included 55 families and 301 species for which life-history and behavioral data were available. This portion of the avian phylogeny contained 30% species classified as colonial, and in all possible reconstructions of the evolution of coloniality, solitary nesting was ancestral. Coloniality evolved at least 21 separate times, and there were at least eight reversals from colonial to solitary breeding within this phylogeny. Colonial nesting thus appears to evolve rather easily.

Rolland *et al.* (1998) found that coloniality evolved in most avian lineages prior to their occupancy of marine habitats. This interesting result runs counter to the prevailing view that species living in marine environments have to be colonial because nesting sites (suitable islands and coastlines) are limited (see Section 4; Wittenberger and Hunt, 1985; Lack, 1968). Rolland *et al.*'s (1998) analysis suggests that coloniality and the mechanisms of food-finding associated with it (see Section 6) allowed species to invade marine habitats where food is likely to be too patchy and unpredictable to be exploited by solitary breeders. This supports the view, for which data are accumulating (see Section 6.3), that social foraging is strongly associated with coloniality and may be a causative factor in some species. The role of predation in the evolution of coloniality was unclear, with no significant patterns between the degree of exposure to nest predators and the evolution of coloniality across the avian phylogeny examined (Rolland *et al.*, 1998). Similarly,

life history traits, such as body mass and clutch size, did not correlate with coloniality after controlling for phylogenetic effects (Rolland *et al.*, 1998). Rolland *et al.*'s results were confirmed by Beauchamp (1999a), whose study of 29 pairs of congeners included both a colonial and solitary species. The obvious message is that coloniality in birds does not reflect phylogenetic constraints and probably evolves rather easily in response to ecological factors. This conclusion validates the interest in trying to understand the costs and benefits of coloniality and the factors promoting colonial nesting in a given species, but it also portends difficulty in arriving at a single general explanation that applies across birds. In a phylogenetic analysis of communal roosting in birds, Beauchamp (1999b) also concluded that social foraging was the most likely causative factor associated with grouping.

Phylogenetic methods were also used to study the relationship between coloniality and mate retention in waterbirds (Dubois *et al.*, 1998). Using methods similar to Rolland *et al.* (1998) and based on the Sibley and Ahlquist (1990) phylogeny, with some modifications, Dubois *et al.* (1998) found that degree of coloniality and probability of switching mates between years were positively correlated within the avian phylogeny examined (the Sphenisciiformes, Procellariiformes, Pelecaniiformes, Phoenicopteriformes, Ciconiiformes, and Charadriiformes). Within these groups, dense coloniality and frequent divorce between seasons appears to be the ancestral state. Dubois *et al.* (1998) suggest that reversals to a low degree of coloniality occurred before mate fidelity developed, and both may be related to occupancy of stable habitats by some colonial species (see Section 8).

#### 4. LIMITATION OF BREEDING SITES

One of the most pervasive themes in the study of avian coloniality is that colonies form because suitable breeding sites are limited, and birds must aggregate at the few sites that do exist. This can be traced probably to Lack (1968, 1967, 1966, 1954), who asserted that many colonial birds, especially waterbirds, are limited by availability of nesting sites. When we began our studies of coloniality 20 years ago, several people declared swallows almost certainly were colonial because their nesting sites were limited and therefore the problem was not interesting. As we were to discover, however, the widespread and largely uncritical belief that coloniality often results from a shortage of breeding sites was based on presumption and supported by little empirical evidence.

The notion of site limitation encompasses several distinct forms

(Brown and Brown, 1996). Some species may require specialized nesting sites that are relatively uncommon, such as the twilight zones of caves in the case of Barn Swallows and Cave Swallows (*Petrochelidon fulva*) (Brown and Brown, 1999a; West, 1995), cliff faces with the appropriate degree of soil compactness in the case of Bank Swallows (Huhta, 1999), or abandoned woodpecker holes in the case of many secondary cavity nesters. Sites may also be limited in the sense that a species uses a relatively common substrate (e.g., the ground) but only a few sites are safe from predators; this appears to be the case for many waterbirds, especially herons and egrets, and other species such as Boat-tailed Grackles (*Quiscalus major*; Post, 1994; Schmutz *et al.*, 1983; Wittenberger and Hunt, 1985; Burger, 1981; Wittenberger, 1981; Buckley and Buckley, 1977; Lack, 1968, 1967). The form of site limitation most often thought of is that of pelagic seabirds that occur in areas with relatively little land mass. These birds are presumably restricted to nesting on isolated islands which tend to be uncommon relative to the marine environments they occupy (Kaiser and Forbes, 1992; Wittenberger, 1981; Lack, 1968, 1967). When colonial nesting is a response to limited habitat, birds may not gain any active advantage from grouping (such as better foraging or avoidance of predators). However, the inevitable costs of coloniality may still be important, and the result can be a decline in fitness for birds occupying larger colonies (see Section 7.1).

One of the few convincing demonstrations of nesting-site limitation was Kaiser and Forbes' (1992) study of burrow-nesting alcids that compared used and unused sites. Most of the estimated 2 million alcids on the northern Pacific coast of North America nest on fewer than 2% of the 6500 coastal islands in the region. Islands chosen are not ones that are free of predators, as conventional wisdom would predict, but rather are ones subject to less frequent rainfall, which limits soil erosion and flooding and enables more stable burrows (Kaiser and Forbes, 1992). Islands chosen also seem to be situated in colder and more saline water, conditions that promote marine productivity and thus may provide favorable foraging conditions for alcids.

However, the Kaiser and Forbes (1992) study is the exception, and there are relatively little data from other species clearly demonstrating that coloniality results from a shortage of breeding sites. Part of this stems from the twin difficulties of defining objectively what features make a "suitable" nesting site and surveying the habitat over a large enough spatial scale to determine that such sites are indeed "limited" relative to the number of potentially breeding birds. The circular logic behind many presumptions of nesting-site limitation is that only sites in use are suitable and therefore the animals are colonial because only

a few sites exist (Brown and Brown, 1996). While numerous studies on colonial birds have concluded that colonies form due to limited nesting sites (Davis and Brown, 1999; Huhta, 1999; Post, 1994; Szep, 1991; Stutchbury, 1991; Emms and Verbeek, 1989; Shields and Crook, 1987; Robinson, 1985; Schmutz *et al.*, 1983; Buckley and Buckley, 1980a, 1977; Houston, 1976; Snapp, 1976; Coulson, 1971; Lack, 1968, 1967), none of these studies quantified suitability of used and unused nesting sites or undertook thorough habitat surveys to document site limitation. Even when used and unused sites are characterized, there are problems with knowing if the variables measured are the relevant ones and thus important to the birds themselves. For example, a study of loosely colonial Red-billed Choughs (*Pyrrhocorax pyrrhocorax*) found physical differences between cliffs that were and were not occupied, but unused cliffs still had some apparently suitable nesting sites, suggesting that other factors caused the birds to aggregate (Blanco *et al.*, 1998).

Despite the difficulties of directly demonstrating a link between coloniality and shortage of nesting sites, indirect methods can sometimes be highly suggestive. For example, cases in which reproductive success is highest for solitary nesters and declines in larger colonies (see Section 7.1) may be instances of site-limited coloniality. In these instances individuals are apparently gaining no benefit from colonial nesting (other than simply being able to breed) yet are still paying the costs of crowding. A caveat, however, should be that colonial birds limited by nesting sites do not always show reduced success in larger colonies (see Section 7.1; Huhta, 1999). For species that use artificial structures such as nest boxes or bridges, amount of nesting substrate can be objectively measured and related to colony size; in Cliff Swallows (*Petrochelidon pyrrhonota*), total amount of concrete substrate for nest attachment at a site did not correlate with colony size, suggesting that nesting-site limitation at least within colonies is not important (Brown and Brown, 1996).

Nest spacing distance is another approach to studying site-limitation. Birds who gain little from associating with conspecifics should spread themselves as far apart as space allows to avoid the inevitable costs of crowding. Muldal *et al.* (1985) experimentally increased the number of nest boxes for loosely colonial Tree Swallows (*Tachycineta bicolor*) and found that the swallows settled in lower density when more nesting sites were available. Possibly these birds prefer to breed at low densities and are forced into colonial nesting by site availability. When nesting sites cannot be manipulated, preferred nest spacing might be easiest to observe among the first arrivals at an uncrowded colony site; later arrivals can be constrained in where they can settle by the presence of

birds already established. Brown and Brown (2000a) measured nest spacing of Cliff Swallows that first arrived at uncrowded colony sites and compared those distances with ones expected if birds were trying to maximize the distance between neighbors. They found that the first birds settled closer together than expected. The results were consistent with Cliff Swallows not being forced into colonies by limited nesting sites, as other data suggest (Brown and Brown, 1996). In contrast, in the putatively site-limited Purple Martin (*Progne subis*), birds generally settled so as to maximize the distance between themselves and other residents (C. Brown and M. Brown, unpublished data).

The belief that a shortage of suitable nesting sites commonly leads to avian coloniality needs to be rethought and re-evaluated with data. Even among seabirds, long thought to be colonial because island-like nesting sites are presumably scarce, the relationship between site-limitation and coloniality is unclear in light of Rolland *et al.*'s (1998) phylogenetic analyses indicating that coloniality in these taxa arose prior to their invasion of the presumably site-limited marine habitats.

## 5. THE COSTS AND BENEFITS OF COLONIALITY

Coloniality clearly affects an animal's individual fitness because of both the costly and beneficial consequences of close proximity of conspecifics. In the well-studied Cliff Swallow, 13 costs and 13 benefits were identified (Brown and Brown, 1996). There have been two main approaches to studying the costs and benefits of coloniality. One has been to compare the behavior and population biology of solitary and colonial nesting individuals of the same species (Sasvari and Hegyi, 1994; Wiklund and Andersson, 1994; Gotmark and Andersson, 1984; Snapp, 1976), an approach that has proven feasible in species such as Mew Gulls (*Larus canus*), Fieldfares (*Turdus pilaris*), or Barn Swallows where relatively high numbers of individuals exhibit each type of breeding system. In this case, direct inferences may be drawn about the putative advantages and disadvantages of colonial versus solitary nesting and the net effect on fitness of each determined (see Section 7.1). Species that exhibit frequent solitary and colonial nesting may represent a current transitional state (Siegel-Causey and Kharitonov, 1990), and thus their ecology may be particularly key to understanding the evolution of coloniality.

More common, however, are species in which relatively few or no individuals nest solitary (the transition to coloniality has been made)

but in which colonies vary considerably in size (Brown *et al.*, 1990). For these species, the traditional approach has been to measure putative costs and benefits of coloniality as a function of colony size (Brown and Brown, 1996, 1987, 1986; Wiklund and Andersson, 1994; Møller, 1987; Shields and Crook, 1987; van Vessem and Draulans, 1986; Robinson, 1985; Veen, 1977; Hoogland and Sherman, 1976). This represents a natural experiment in which the effect of variable numbers of conspecifics can be gauged and the overall effect of group size on fitness can be determined. Colony size is usually defined as the number of conspecifics breeding at a site. However, Burger (1981) pointed out that many ciconiiforms, in particular, form mixed-species colonies, and because these species are often similar ecologically, functional colony size may sometimes include the total number of individuals of related species.

Some researchers have sought to classify the benefits of coloniality into those that originally caused animals to form colonies (causative factors) and those that work to maintain coloniality once individuals have clustered (maintenance factors; Rolland *et al.*, 1998; Danchin and Wagner, 1997; Brown and Brown, 1996; Richner and Heeb, 1996; Siegel-Causey and Kharitonov, 1990; Shields *et al.*, 1988). The implicit assumption has been that it is more important to identify causative factors. Some group-size effects observed in colonial birds may be secondary consequences of clustering that developed only after colonies formed (e.g., increased opportunities to engage in extra-pair mating or brood parasitism; Section 5.2), while others were probably involved in the transition from solitary to colonial nesting (e.g., increased foraging efficiency; Section 6). However, clearly distinguishing between causative and maintenance factors has been difficult; even phylogenetic analyses have not unambiguously identified historical causative factors (Section 3). Birds might have originally formed groups for one reason, but once in a colony other incidental benefits of colonial nesting and the costs of crowding will almost always apply. The original advantage to grouping may not itself be sufficient to maintain coloniality in the face of the inevitable disadvantages, and it is the secondary benefits that keep the net fitness effect of coloniality positive (Brown and Brown, 1996; Korpachena, 1991). Unfortunately, when we measure the contemporary "benefits" of coloniality in the field, we cannot always know whether we are measuring a causative or maintenance factor. The attempt to classify benefits of coloniality into these two types has stifled progress because it focuses on the unanswerable question of which one(s) caused initial clustering. Attention should be paid to how all costs and benefits, regardless of putative origin, affect net fitness of colonial individuals.



### 5.1. Ectoparasite and Disease Transmission

The deleterious consequences of colonial nesting had rarely been appreciated before Alexander (1974, 1971) emphasized that increased ectoparasite and disease transmission and increased competition for local resources are probably universal. Most attention since then has been given to the effect of group size on prevalence of parasitism; surprisingly few studies have looked at how competition for resources varies among colonial species or at the other costly consequences of clumped nesting (see Brown and Brown [1996] for a treatment of other costs).

Early work established that birds nesting in large colonies generally have higher per-capita rates of ectoparasitism than conspecifics in small colonies or those in solitary nesting (Møller, 1987; Shields and Crook, 1987; Brown and Brown, 1986; Hoogland and Sherman, 1976). Social species in general tend to be associated with more ectoparasites (Cote and Poulin, 1995; Poulin, 1991). Most studies have focused on hemiparasitism, with topographic parasites such as ticks, fleas, mites, and cimicid bugs, which are large, easy to count, usually nest-site based, and horizontally transmitted. Work in the 1970s also demonstrated that blood-feeding ectoparasites can have deleterious consequences on nestling survival (Chapman and George, 1991; Moss and Camin, 1970), findings since replicated by many other studies of colonial birds (Loye and Carroll, 1991; Møller, 1990; Shields and Crook, 1987; Brown and Brown, 1986). Although the widely cited studies were done on various species of swallows, there is now universal acceptance that increased parasitism is a cost of coloniality in birds (for nonpasserine taxa, see Merino *et al.*, 1999; Gauthier-Clerc *et al.*, 1998; Boulintier and Danchin, 1996; Moore *et al.*, 1988; Duffy, 1983; King *et al.*, 1977; Feare, 1976; Jennings and Soulsby, 1958).

More recent work has revealed that ectoparasites have effects on colonial birds beyond those on nestling survival and reproductive success. Parasites of adult birds are generally hard to quantify (Clayton and Walther, 1997), but in at least one colonial species (the Cliff Swallow) ectoparasitism lowers annual survivorship of adult birds in addition to that of nestlings (C. Brown *et al.*, 1995). Also in Cliff Swallows, natal dispersal is apparently influenced by the extent of ectoparasitism a bird experiences as a nestling, with birds parasitized by fleas tending to settle in colonies other than the natal one for their first breeding attempt (Brown and Brown, 1992). As a result, ectoparasitism may play a fundamental role in colony-site selection, with birds dispersing away from infested sites (Brown and Brown, 1996). Work on swallows has shown that birds actively assess nest sites within colonies early in the spring

(Brown and Brown, 1996, 1986; Møller, 1990) and avoid nests infested with fleas, mites, and cimicid bugs. Given the increased prevalence of parasites and pathogens in large colonies and their ability to overwinter at sites in the absence of their bird hosts (Brown and Brown, 1996; LITERAK *et al.*, 1996; Danchin, 1992), the dynamics of colony-site use may be tied to patterns of ectoparasitism in general. Ectoparasitism could be a determinant of annual site suitability in colonial birds.

The belief that ectoparasites increase with colony size has been widely accepted even though there is no information to explain how ectoparasitism increases in large colonies. Large colonies presumably present more opportunities for horizontally transmitted ectoparasites (once introduced into a colony) to disperse among individuals and find suitable hosts, as birds spread parasites through intentional or incidental physical contact with each other, or by close nest spacing. Large colonies may also present a more attractive "target" for dispersing parasites; parasites may be more likely to be introduced into a large group (Brown and Brown, 1996). No systematic studies have measured transmission probabilities for ectoparasites, either within or between colonies, and thus we do not know which mechanisms tend to be important in general. Bird colonies present many opportunities to study parasite transmission and provide epidemiological models for human cities (Keeling and Grenfell, 1997; Black, 1966). Similarly, we know little about how the prevalence of disease-causing pathogens varies with colony size in birds, although the observed outbreaks of avian cholera and other sicknesses among waterfowl concentrated in small areas (Wittenberger and Hunt, 1985) suggest that diseases may be more likely in large colonies.

Although ectoparasitism seems to be a general cost of breeding in colonies for birds, for other taxa there is evidence that ectoparasites and pathogens sometimes may be avoided more effectively through increases in group size. This tends to be the case when both the parasites and hosts are mobile and not confined to particular sites, and when the parasites do not reproduce within the host nests. By clustering, individuals may dilute the per-capita rate of attack by parasites, such as blood-feeding flies, in a manner analogous to avoiding predators through encounter-dilution and selfish herd effects (Mooring and Hart, 1992; Section 5.3.3). This form of parasite avoidance is commonly seen in large herding mammals, but the only reported example in birds comes from Magellanic Penguins (*Spheniscus magellanicus*), in which prevalence of parasitism by ground-dwelling fleas decreased with colony size (J. L. Tella, personal communication). There is also both theoretical (Watve and Jog, 1997) and empirical work (on fishes; Cote and Cross,



1993) suggesting that between-colony transmission of parasites may at times be reduced whenever hosts aggregate in large groups and thereby increase the average distance between infected individuals. Simulations by Watve and Jog (1997) indicate that in some cases intermediate (or large) group sizes may be best for reducing the probability of pathogen transmission. Whether their theory applies to bird colonies is unknown, but clearly we should not assume that ectoparasitism always increases in large breeding groups of birds.

## 5.2. Misdirected Parental Care

Coloniality presents opportunities for individuals to parasitize the reproductive effort of other individuals, and the probability that an individual will misdirect its parental care to the offspring of an unrelated individual often increases with colony size (Brown and Brown, 1996). Extra-pair mating, intraspecific brood parasitism, and the mixing of mobile young are the main forms of misdirected parental care possible in bird colonies. Traditionally these have been viewed through the eyes of the individual whose parental care is parasitized and regarded as costs of coloniality, but the opportunity to parasitize others in a colony may also be an important benefit of group living.

### 5.2.1. Extra-Pair Mating

With breeding individuals spatially concentrated, colonies present many opportunities for individuals to engage in extra-pair copulation. Consequently, researchers have regarded the greater risk of a male being cuckolded in a large colony as a potential cost of coloniality (Westneat *et al.*, 1990; Møller, 1985; Hoogland and Sherman, 1976). That extra-pair copulations seem to be common in colonial birds in general was first appreciated by Gladstone (1979), and later analyses have confirmed both that colonial species are more likely to engage in extra-pair copulations than related solitary species and the frequency of extra-pair copulation often increases with colony size or breeding density (Hoi and Hoi-Leitner, 1997; Brown and Brown, 1996; Møller and Birkhead, 1993; Birkhead *et al.*, 1992; Hatchwell, 1988; Emlen and Wrege, 1986; Møller, 1985; Hoogland and Sherman, 1976). Although not addressed theoretically, the increased likelihood of extra-pair copulation in colonial species seems to result from the proximity of multiple potential partners (Westneat and Sherman, 1997) and possibly also because of greater reproductive synchrony among individuals in colonial species, which itself may promote extra-pair copulation (Stutchbury and Morton, 1995; Birkhead and Møller, 1992; cf. Weatherhead, 1997).

However, little information is available to evaluate whether the observed increase in extra-pair copulation in large groups represents a cost of coloniality. Extra-pair copulations may not be costly to male mates if they do not result in fertilizations. In highly colonial Ross's Geese (*Chen rossii*) and Snow Geese (*C. caerulescens*), which together show one of the highest reported frequencies of extra-pair copulations in birds at 46–56% of all attempted copulations, only 2–5% of young are of extra-pair paternity (Dunn *et al.*, 1999). In colonial Humboldt Penguins (*Spheniscus humboldti*), 17.9% of copulations were extra-pair, but none resulted in fertilizations (Schwartz *et al.*, 1999). A comparative analysis across 72 bird species with data (largely molecular) on paternity showed no effect of coloniality on nesting density or rates of extra-pair fertilization (Westneat and Sherman, 1997); breeding synchrony also had no effect. Increased rates of extra-pair copulation in colonial birds apparently do not translate into greater probabilities of producing extra-pair young, possibly because of more frequent intra-pair copulation that ameliorates the cost to males of extra-pair mating by their mates (Møller and Birkhead, 1993).

In evaluating the net effect of extra-pair mating on fitness of colonial birds, it is necessary to know whether extra-pair copulations are perpetrated by resident males in the colony or by nonresidents who enter the colony to mate with females. If only resident males engage in extra-pair mating, then the average reproductive success within the colony will not change; only the variance among male colony residents will be affected. While this may be costly for the cuckolded males, other males will benefit, and there will be no net reduction in average fitness between colonial versus solitary males and no selection for or against coloniality *per se*. Only if nonresidents achieve extra-pair fertilizations with females in colonies will there be a net fitness cost of coloniality for males.

Although a colony's male residents often seem to engage in extra-pair copulation, we presently have little data on how often male participants in extra-pair mating are nonresidents of a colony. In Barn Swallows, nonbreeding males visit colonies (Crook and Shields, 1985) and possibly engage in extra-pair copulations with female residents. Observational studies of Cliff Swallows indicate that male nonresidents come to colonies possibly to force or solicit extra-pair copulations (Brown and Brown, 1996), and the early-season visits to colony sites by nonbreeders in some seabirds (Kharitonov and Siegel-Causey, 1988) may serve the same purpose. The best (but most difficult) way to identify perpetrators of extra-pair copulations is to have molecular parentage data for all male colony residents. This allows identification of any extra-pair offspring as having originated from either inside or outside the colony. DNA

fingerprinting studies suggested that some young were sired by males from outside the colony in Boat-tailed Grackles (Poston *et al.*, 1999), and unpaired floater males achieved paternity of about 15% of nestlings in noncolonial Stitchbirds (*Notiomystis cincta*; Ewen *et al.*, 1999).

Extra-pair copulation simultaneously represents a cost and a benefit to different individuals within the same colony. More recent emphasis has been on how both males and females might benefit from coloniality through the greater opportunities to seek extra-pair fertilizations and how these advantages might promote the evolution of coloniality (Wagner, 1997, 1993; Brown and Brown, 1996; Morton *et al.*, 1990). This is treated in Section 8.

Although unrelated to the fitness costs and benefits of coloniality, an interesting consequence of higher rates of extra-pair mating in colonial birds could be increased rates of species diversification (Moore and Møller, 1996; Birkhead and Møller, 1992). This occurs because, with relatively few males achieving a high proportion of fertilizations (e.g., Wagner *et al.*, 1996), colonial birds may have smaller effective population sizes and consequently more rapid rates of evolution. Colonial populations thus may be better able to track environmental changes and show increased local adaptability, which can lead to more rapid speciation. This hypothesis requires a direct relationship between rates of extra-pair copulation and extra-pair fertilization, which, as noted above, has not been found. Furthermore, a phylogenetic analysis of 2700 species using the Sibley and Ahlquist (1990) phylogeny found no association between the number of species in a clade and whether the clade is colonial or not (Moore and Møller, 1996). For these reasons the hypothesis of increased diversification among colonial birds seems unlikely to apply, although Rosenzweig (1996) argued on technical and philosophical grounds that Moore and Møller's (1996) analyses do not necessarily refute the hypothesis.

### 5.2.2. Intraspecific Brood Parasitism

Females may parasitize the reproductive effort of conspecifics within a colony by laying eggs in others' nests. In one species (Cliff Swallow), females are known to transfer eggs in their bills between nests, also a way to parasitize nests (Brown and Brown, 1988). Brood parasitism allows a female to supplement her reproductive output by increasing the number of her eggs that ultimately produce young, reduce the costs of reproduction by foisting parental care of her young onto others, or in some cases achieve limited reproduction when conditions do not allow her to establish her own nest (reviewed in Lyon and Everding, 1996;

Andersson, 1984). As with extra-pair mating, how nesting dispersion per se should affect rates of intraspecific brood parasitism has not been studied theoretically (see Eadie and Fryxell, 1992), but the close proximity and temporal synchrony of nests within colonies presumably increases a parasite's access to potential host nests and has led to predictions that parasitism of conspecifics should be more frequent in colonially nesting species (Brown and Brown, 1996, 1991; Rohwer and Freeman, 1989; Freeman, 1988; Brown, 1984; Hoogland and Sherman, 1976; Hamilton and Orians, 1965).

Although intraspecific brood parasitism has been documented in many birds (Rohwer and Freeman, 1989; Yom-Tov, 1980), relatively few studies have measured it in relation to colony size or compared colonial versus solitary populations of the same species. In both Cliff Swallows and Barn Swallows, the percentage of nests with at least one parasitic egg of a conspecific increased significantly with colony size (Brown and Brown, 1996, 1989, 1988; Møller, 1987; Brown, 1984), with 25–40% of nests in some colonies being parasitized. In Wood Ducks (*Aix sponsa*), 95% of nests were parasitized, multiple times, in an area where nesting boxes had been provided in high density and large numbers of ducks nested within sight of each other (Semel and Sherman, 1986). In a study of Eared Grebes (*Podiceps nigricollis*), the largest colony with the highest nest density had 68% of nests parasitized by conspecifics, compared with 14% and 38% in two smaller colonies (Lyon and Everding, 1996). In another study of Eared Grebes, brood parasitism occurred in 11.8–18.9% of nests in colonies with high nest density compared to 0–6.8% of nests in colonies with lower nest density (Hill *et al.*, 1997). However, Hoogland and Sherman (1976) found no effect of colony size on rates of brood parasitism in Bank Swallows, and Rohwer and Freeman's (1989) comparative analysis found no strong association between coloniality and intraspecific brood parasitism for the species for which they had information. Data on more species (designed specifically to measure parasitism as a function of colony size) are necessary before we can conclude that higher rates of brood parasitism occur generally among colonially nesting birds.

Although no one has explored formally how coloniality should affect rates of brood parasitism, it is likely that there are density-dependent effects on brood parasitism. Simulation studies by Eadie and Fryxell (1992) show that with a fixed frequency of conspecific brood parasitism, a local increase in the total number of females can increase the fitness of parasites because more potential hosts are available. A decrease in the number of females available may lower the density of hosts to a level where fitness of parasites is less than that of non-

parasites. The result is that the equilibrium frequency of brood parasitism changes in a nonlinear fashion with the total density of females. This emphasizes the need for studies designed to measure local availability of hosts to potential parasites. We cannot assume that a large colony automatically contains more potential hosts because it may also contain more potential parasites that compete for the available host nests. There may also be physical constraints on the ability of parasitic females to locate potential hosts; for example, nests at the opposite end of a large colony may be functionally unavailable as hosts to parasites from the other end of the colony. In Cliff Swallows, parasitic females can monitor only a subset of the colony's nests and even fewer of those are suitable spatially and temporally as potential host nests (Brown and Brown, 1996, 1991).

Assuming that brood parasitism is more likely in colonies, we still face some of the same issues encountered for extra-pair mating in determining whether it represents a serious cost (or benefit) of coloniality. Brood parasitism is usually considered costly because hosts raise unrelated offspring, but are there other costs to being parasitized? Increased brood sizes resulting from brood parasitism may impair subsequent survival of host offspring or parents (Nee and May, 1993; Yamauchi, 1993). This seems to be true for waterfowl, who add multiple eggs to host nests, but few chicks survive (Semel and Sherman, 1986). Yet in the Cliff Swallow, survival analyses demonstrated that hosts suffer no long-term costs of being parasitized by a conspecific (Brown and Brown, 1998). This may depend in part on the natural history of the species involved: Ducks parasitize nests without removing eggs, often causing unusually large clutches that cannot be effectively cared for, whereas Cliff Swallows brood-parasitize nests in ways that do not result in larger than average broods (Brown and Brown, 1996, 1989, 1988). The degree to which brood parasitism represents a cost of coloniality thus will depend on how costly parasitism is for hosts.

We also need to know which females—residents or nonresidents—engage in brood parasitism. If the behavior is perpetrated solely by resident females who also maintain nests of their own, as do Cliff Swallows and Barn Swallows (Brown and Brown, 1989; Møller, 1987; Brown, 1984) and Northern Masked Weavers (*Ploceus taeniopterus*; Jackson, 1993), it may change only the variance in reproductive success among nests in the colony and not represent a cost, on average, of coloniality. But, as with extra-pair mating, if nonresidents recruit to colonies to brood-parasitize nests, fitness of colony nesting individuals will be reduced relative to solitary nesting birds who are not parasitized. Little is known in general about whether females without nests are

brood parasites or whether "professional" parasites might come recruiting to colonies, although Lyon (1993) reported parasitism by nonresident, floater females in American Coots (*Fulica americana*).

The benefits of brood parasitism, at least in the well studied swallows, are more obvious. Parasitism of other nests by colony residents is a supplemental reproductive strategy that seems to generally lead to higher annual reproductive success; that parasites themselves also have higher annual survivorship seems to indicate they may be superior quality birds to start with (Brown and Brown, 1998). The increase in brood parasitism with colony size (e.g., Brown, 1984) could suggest that potential parasites indeed have more opportunities to parasitize nests in larger colonies and for that reason coloniality would be advantageous for them. However, another interpretation could be that the superior birds that parasitize nests settle preferentially in large colonies for other reasons, and thus brood parasitism itself might not be a direct consequence of coloniality. Manipulating colony size after birds have settled may be the only way to distinguish between these possibilities.

### 5.2.3. Mixing of Mobile Offspring

In most colonial birds, nesting is relatively synchronous, and a consequence is that multiple young from different nests become mobile or they fledge simultaneously. With nests often in close physical proximity to each other, offspring of similar age from different parents have frequent opportunities to mix either in brood assembly areas or at the nest itself. There is a large literature on "adoption" in animals (reviews in Pierotti, 1991; Riedman, 1982), with many studies showing parents on occasion will care for unrelated chicks who join their brood, including feeding the adoptive young (Tella *et al.*, 1997; Brown and Brown, 1996). However, that some species kill unrelated young that try to join their brood, and that adoptive parents sometimes have lower total reproductive success than nonadoptive parents, suggest there are costs associated with adopting extra chicks (K. Brown *et al.*, 1995; Pierotti, 1991; Carter and Spear, 1986). If coloniality increases the chances of caring for unrelated young that join one's brood either before or after fledging, this may represent another cost of colonial nesting.

Few studies have quantified brood mixing in relation to colony size. Pierotti's (1991) review revealed that 25 of 30 species for which brood adoptions are known were either colonial nesters or bred in cooperative family groups. This suggests that coloniality enhances the occurrence of chick mixing or at least its detection. Brown and Brown's (1996) work on Cliff Swallows is the only study that has examined mixing of young

specifically in relation to group size. Juvenile swallows often return to a colony and intrude into nests of other parents, often ones with smaller nestlings, and take the food brought by their adoptive "parents." In most cases the adults accept the foreign young and readily feed them as long as they remain in the nest. The frequency of this sort of kleptoparasitism (food stealing) increases with colony size (Brown and Brown, 1996). Juveniles that are still dependent on their parents for food and some that are independent come to colonies in apparent attempts to steal food. How serious a cost this is for offspring and parents of nests parasitized is unknown in Cliff Swallows, so its importance as a cost of coloniality cannot be evaluated, although there is evidence that caring for adoptive young in gulls can be costly for parents (K. Brown *et al.*, 1995; Carter and Spear, 1986). That kleptoparasitic Cliff Swallows from smaller colonies move to larger colonies suggests mixing of young may reduce average fitness of birds in colonies, relative to solitary nesters, and that it may do more than just change the variance in fitness within a colony.

The benefits of adoption and kleptoparasitism for a chick are seemingly obvious: When accidentally separated from one's parents or when poorly provisioned by one's parents, chicks can increase their food intake and survival prospects by joining another brood and soliciting food there (K. Brown *et al.*, 1995; Redondo *et al.*, 1995; Pierotti, 1991). Mixing thus should generally be advantageous for young, unless parents can recognize their own chicks and actively repulse (sometimes injuring or killing) intruders in the brood. The opportunistic cannibalism shown by some colonial birds, especially gulls (reviewed in Wittenberger and Hunt, 1985), presumably is an effective deterrent to adoptions in some species.

When mixing of young is not in the best interests of parents whose care would be parasitized and yet opportunities for unintended adoptions abound, parent-offspring recognition systems should develop (Beecher, 1991, 1988). Colonial animals generally show some ability to recognize their own offspring, at least after fledging when mixing is most likely, when compared to ecologically similar but solitary nesting species (Medvin *et al.*, 1993, 1992; Beecher *et al.*, 1981a,b). However, even among species with the ability to recognize offspring in some contexts, such as Cliff Swallows (Stoddard and Beecher, 1983), mistakes often happen and adoptive chicks are accepted. An information analysis of begging calls in Cliff Swallows (used by parents to identify their own chicks) suggests that parents can readily recognize their own young as long as group size is about 80 birds or fewer (Medvin *et al.*, 1993). But structural limitations in the begging call provide a finite set of distinguishable signals. When group size goes above 80, parents begin to lose

their discriminatory ability amid the inevitable similar signals from other chicks; by the time group size reaches 500 birds, parents are able to find their own young only about 50% of the time (Medvin *et al.*, 1993). Since Cliff Swallow creches, in which young assemble after fledging, often exceed 500 birds, young may often be misidentified. In other cases, it takes parents longer to find their own offspring because they must search through a large group (Brown and Brown, 1996). Thus, the presence of parent-offspring recognition in colonial species does not automatically prevent unintended chick mixing and brood adoptions, and this cost of coloniality may be inevitable in very large colonies. Further work is needed, however, to quantify this cost in general and identify those species in which it applies. King Penguin (*Aptenodytes patagonicus*) chicks, which recognize parents by the adult birds' calls, seem to have no difficulty identifying their own parents in very large and noisy colonies (Jouventin *et al.*, 1999).

Brood adoptions are not always costly in colonial species. In the colonial Common Eider (*Somateria mollissima*), chicks from several females often mix together in creches soon after hatching (Munro and Bedard, 1977a,b). This fascinating behavior is poorly understood and may be explainable in part by kin (indirect) selection, but it appears that females do not discourage mixing among young and may even compete among themselves for each other's chicks. The consequence is formation of fewer, much larger groups of young tended primarily by one female. Larger creches, though more often attacked by gull predators, tend to offer advantages through dilution and possibly selfish herd effects (see Section 5.3.3), and thus a female's own offspring may have a greater probability of escaping predation (Munro and Bedard, 1977a,b). Brood adoptions in general may be less costly, and perhaps advantageous in terms of avoiding predators, in highly precocial species (particularly waterfowl) in which young do not require extensive nonshareable parental investment such as feeding (Eadie *et al.*, 1988).

### 5.3. Predation-Related Effects

Traditionally, the avoidance of predators has been viewed as a primary reason that birds form flocks during the nonbreeding season and colonies during the breeding season (Brown and Brown, 1996; Wiklund and Andersson, 1994; Elgar, 1989; Forbes, 1989; Wittenberger and Hunt, 1985; Pulliam and Millikan, 1982; Burger, 1981; Hoogland and Sherman, 1976; Alexander, 1974, 1971; Pulliam, 1973). Grouping of prey may decrease a predator's success in a variety of ways: (1) Incoming predators may be more likely to be detected (or detected farther away),

giving a group more time to take evasive or defensive action; (2) a group may more effectively mob a predator and deter it from attacking; and (3) a group through several means may reduce an individual's own probability of being the one taken by a predator if the predator does attack. The extensive work done on how nonbreeding flocks (often foraging groups) benefit from group living (Beauchamp, 1998; Lima and Dill, 1990; Elgar, 1989) has seemed applicable to breeding colonies and has perhaps led to the belief that reduced predation is a widespread advantage of colonial nesting (Brown and Brown, 1996). In a few cases, the principal function of coloniality indeed seems to be to reduce nest predation, as shown for example by artificial nest experiments in Mew Gulls (Gotmark and Andersson, 1984). However, the data purported to show antipredator benefits of coloniality in most species are equivocal. Many of these data (based solely on measures of nesting success; Section 5.3.3) have not ruled out alternative explanations. Also, recent empirical work now suggests, perhaps more clearly, that coloniality often leads to higher rates of predation.

### 5.3.1. Vigilance

A reduction in an individual's time spent scanning for predators with increased group size is one of the most frequently reported relationships in animal behavior (Roberts, 1995). Presumably this results from both the increased probability that a predator will be detected by some group member (Bertram, 1980; Powell, 1974; Pulliam, 1973) or the decreased probability that a given individual will be the one attacked if a predator does appear (Foster and Treherne, 1981; Hamilton, 1971). Group size itself is usually thought to cause the change in vigilance, although relatively few studies have controlled for effects potentially correlated with group size, which may themselves affect vigilance (such as density of food supplies, distance to cover, age, sex, and observer proximity; Beauchamp, 1998; Roberts, 1996; Poysa, 1994; Elgar, 1989). Most of the empirical work on vigilance in birds has been done on foraging groups, usually during the nonbreeding season or in situations away from breeding sites.

It has often been assumed that birds nesting in colonies receive the same vigilance-related advantage of being less likely to fall victim to a predator; also, as time spent scanning for predators diminishes, time available for other nesting activities should increase (Brown and Brown, 1987). Hoogland (1981, 1979) and Kildaw (1995) measured individual alertness of prairie dogs in colonies, but to our knowledge not a single study on birds has measured vigilance (scanning rates) of individuals

at a breeding colony. Two studies, both on Cliff Swallows, inferred vigilance based on the distance from the colony at which model predators were detected during experimental presentations. In one case using avian predator models, no effect of colony size on the distance of detection was found (Wilkinson and English-Loeb, 1982); in the other case using snake predator models, detection distance increased with colony size (Brown and Brown, 1987). A study of Barn Swallows found that in larger colonies, less time elapsed before an initial alarm call was sounded when a stuffed owl appeared (Møller, 1987). Yet despite the general lack of data on vigilance at colonies, we believe that a greater probability of detecting an incoming predator as colony size increases is an automatic consequence of having "many eyes" (Pulliam, 1973) and should apply across most species of colonial birds.

It is not so clear, however, that colonial birds necessarily have more time for other activities, because an individual's total vigilance may not be reduced in colonies. The presence of many nearby conspecifics may cause an increase in scanning directed toward other group members (Goss-Custard *et al.*, 1999; Beauchamp, 1998; Hill *et al.*, 1997; Brown and Brown, 1987; Burger, 1981); for example, males may have to monitor their mates more closely to prevent extra-pair copulation attempts; females may have to watch neighboring females more closely to prevent attempts at nest parasitism by egg laying; and both sexes may have to monitor neighbors closely to prevent theft of nesting material or food, cannibalism of young, or nest-site usurpation. Increased rates of neighbor-directed vigilance may negate any advantage of reduced scanning for predators and potentially represent another cost of coloniality, especially if vigilance significantly interferes with the time available for courtship, feeding, or care of eggs and young. We need time-budget studies to examine colonial versus solitary individuals and birds nesting in colonies of different sizes before we can determine to what degree coloniality affords vigilance-related advantages (or disadvantages) in birds.

### 5.3.2. Deterrence

A characteristic of breeding colonies not generally shared with foraging groups is that colony residents, with nests and offspring to protect, are inclined to mob predators and deter them from attacking. Mobbing usually consists of relatively coordinated flights near a predator by several individuals, often accompanied by alarm-calling and sometimes diving at or aggressive physical contact with the predator. Often there is no active cooperation among mob members, with mob-

bing mostly a summation of responses by multiple individuals whose nests are threatened and who are farthest along in the nesting cycle (Shields, 1984; Smith and Graves, 1978; Horn, 1968). It is presumed mobbing deters a predator either through intimidation, bewilderment and confusion, or notification that it has lost the element of surprise and is thus unlikely to be successful. Mobbing has been observed in many colonial species (Brown and Brown, 1996). Although solitary individuals also may mob, coloniality affords the opportunity for potentially more effective mobbing by virtue of the large number of possible mob members. The larger mobs in colonies also reduce a mobber's personal risk of being attacked and killed by the predator during mobbing (Brown and Hoogland, 1986).

Several studies have shown that the size of mobs increases with colony size or is greater in colonies than at solitary nests (Wiklund and Anderson, 1994; Burger and Gochfeld, 1991; Poiani, 1991; Hoogland and Sherman, 1976). Only two studies to our knowledge, however, have shown clearly that deterrence of predators is related to mob size. In the Yellow-rumped Cacique (*Cacicus cela*), predatory toucans and raptors were more effectively discouraged from colonies by higher numbers of mobbers (Robinson, 1985); and in the Lapwing (*Vanellus vanellus*), survival of artificial nests was positively correlated with Lapwing nest density, apparently because of more effective mobbing of predatory crows by increased numbers of Lapwings (Elliot, 1985). That these two studies involved avian predators may suggest that birds (who often have less body-size advantage relative to their prey) are more likely to be deterred by mobbing than are snake or mammal predators. Avian predators, such as hawks and magpies, are more likely to terminate attacks at Cliff Swallow colonies when mobbed than are snakes (Brown and Brown, 1996). Mobbing does not faze snakes, who proceed to enter a colony regardless of the extent of mobbing directed at them. Type of predator obviously influences whether coloniality affords deterrence advantages. Until more data on the effectiveness of mobbing in and of different species are available, we cannot know whether advantages associated with mobbing represent general benefits of colonial nesting.

### 5.3.3. Dilution of Risk

Another often-cited advantage of group living is that grouping reduces an individual's personal risk of predation by diluting its chances of being the one(s) taken by a predator on a given attack. Most predators cannot eat all of the members of a group on a single attack, and the proportion they can eat usually declines with group size. Thus, colo-

nality can potentially lead to avoidance of predation even in the absence of better predator detection or deterrence.

Dilution of risk can occur in several ways. Individuals can form a selfish herd (Hamilton, 1971), jockeying for sites so as to position other birds' nests between themselves and the potential approach of a predator and thus maximizing the likelihood that the predator will encounter other nests before reaching theirs (Tenaza, 1971; Vine, 1971). In addition to a selfish herd or even in its absence, individuals can synchronize their reproduction, which may satiate predators during a short time period and reduce the statistical likelihood that a given individual or its nest will be preyed upon. The simple numerical advantage of being one of many potential prey when confronted by relatively few predators automatically leads to lower predation risk (e.g., during mobbing; Brown and Hoogland, 1986). These benefits of reduced risk only apply, however, when predators do not recruit to colonies (Ims, 1990) and when they are less likely to detect a group of individuals than an equal number of solitary prey. For example, dilution will not occur in a group of size  $n$  if a predator is  $n$  times as likely to detect and attack a group as a solitary individual (Inman and Krebs, 1987; Turner and Pitcher, 1986).

The degree to which colonial birds dilute their risk of predation through any of these means is not at all clear, despite numerous studies reporting data consistent with dilution effects. Nests near the edge of a colony are commonly reported to be more likely to fail than ones closer to the center, providing apparent support for the notion that colonies act as selfish herds against predation (reviewed in Brown and Brown, 1996; Wittenberger and Hunt, 1985). However, in most cases these data confound spatial effects on predation (the selfish herd) with differences in the quality of individuals nesting near the edge versus the center of a colony. Often, young and inexperienced individuals arrive later and settle on the edges of a colony, and lower nesting success there may be due to the edge birds' inferior condition (Ganter and Cooke 1998; Kharitonov and Siegel-Causey, 1988; Wittenberger and Hunt, 1985; Coulson and Dixon, 1979; Nelson, 1978; Coulson, 1971, 1968). To disentangle the effects of bird quality and spatial position, one needs reciprocal egg- and chick-exchange experiments such as those of Bunin and Boates (1994) on Arctic Terns (*Sterna paradisaea*). They found that both parental quality and spatial position apparently influenced tern success. In other cases, nest failure may be caused by ectoparasites (see Section 5.1), and without controlled fumigation experiments, effects of predation cannot be separated from those of ectoparasitism, which may also vary spatially within a colony (Brown and Brown, 1996).

When predation has been measured, center nests are not always



less vulnerable. For example, in a colony of Least Terns (*Sterna antillarum*), center nests suffered 85.4% predation to Black-crowned Night Herons (*Nycticorax nycticorax*) compared to 54% for edge nests; the herons typically flew directly to the center of the colony to begin feeding (Brunton, 1997). American Crows (*Corvus brachyrhynchos*) at the same site usually took edge nests, emphasizing again that different predators may have different effects on colonies. Experiments in heronries showed that artificial nests near the center were more likely to be preyed upon by Hooded Crows (*Corvus corone*) than were ones near the periphery of a colony (Bellinato and Bogliani, 1995). Central individuals were also more likely to be attacked in fish (Parrish, 1989) and social wasps (Strassmann, 1991).

Many colonial species tend to synchronize their reproduction within a colony, usually more so than would be expected if synchrony was solely a response to seasonal environmental cues (Ims, 1990; Burger, 1981; Gochfeld, 1980). That synchronous individuals tend to be more successful has been known since Darwin (1938), with numerous studies on birds and other taxa showing that breeding success rises during periods of synchrony. Yet once again, the role of predation in producing this pattern is unclear. Synchronous nesting may lead to higher success because periods of synchrony also correspond to periods of peak resource abundance or for climatic or other phenological reasons, or because synchrony affords more opportunities to forage socially (see Section 6; Gochfeld, 1980). Greater success of synchronous breeders may also be an artifact of bird-quality differences between individuals starting at different times of the year; late nesters who are often asynchronous are frequently young and inexperienced (Massey and Atwood, 1981).

Despite a vast amount of literature on reproductive synchrony in birds (see Brown and Brown, 1996; Murphy and Schauer, 1996; Wittenberger and Hunt, 1985), few studies have contained detailed data on the proportionate impact by predators for different degrees of reproductive synchrony (Ims, 1990). In the Cliff Swallow, under natural conditions reproductive success was greatest for the most synchronous nests (as found in many other species), but when ectoparasites were removed by nest fumigation, this effect vanished and predation had no effect (Brown and Brown, 1996). Additional experimental studies of this sort are needed before we can judge whether colonially nesting birds truly dilute their risk of predation by breeding synchronously. The degree of between-colony synchrony is also important, because if the colonies in a given region become active sequentially, multiple predators may switch between them over the course of the season, eliminating some of the advantages associated with satiating a single individual predator

(Ims, 1990). On balance, the evidence that synchronous nesting represents an important antipredator advantage in colonial birds is weak, a point also made by Murphy and Schauer (1996).

### 5.3.4. Attraction of Predators

For a colonial individual's risk of predation to be lowered through better detection, deterrence, the selfish herd effect, or breeding synchrony, a colony has to be proportionately less likely to be attacked than a solitary individual (see Section 5.3.3). Thus, knowing the rate at which predators attack colonies versus solitary nests is critical to determining whether coloniality actually offers a net benefit in avoiding predators or constitutes a cost through greater likelihood of predation.

A bird colony is inherently conspicuous, owing to the synchronized activities of multiple residents as they come and go and the sight, sound, and smell of their young. This has been recognized as a potential cost of colonial nesting or lekking (Phillips, 1990; Sillen-Tullberg, 1990; Wittenberger and Hunt, 1985; Burger, 1984; Wittenberger, 1981; Vine, 1973; Lack, 1968; Kruuk, 1964), and several studies have reported high predation rates by predators at single, large colonies (Brunton, 1997; Donaldson *et al.*, 1995; Burness and Morris, 1993; Cairns, 1992; Szep and Barta, 1992; Ahlen and Andersson, 1970). Avian predators have been observed traveling directly to bird colonies to hunt (Kaiser, 1989), and in fish, larger schools elicit a higher attack rate from predatory fish because of their conspicuousness (Krause and Godin, 1995). Consistent with this in birds, several studies have shown that predation rate increases with colony or group size: in Common Eiders (Munro and Bedard, 1977b), Shelducks (*Tadorna tadorna*; Pienkowski and Evans, 1982), White-browed Sparrow-weavers (*Plocepasser mahali*; Ferguson, 1987), Fieldfares (Wiklund and Andersson, 1994), Black-crowned Night Herons and Little Egrets (*Egretta garzetta*; Bellinato and Bogliani, 1995), Cliff Swallows (Brown and Brown, 1996), and Least Terns (Brunton, 1999; Burger, 1984). Among Sage Grouse (*Centrocercus urophasianus*) and Snowy Plovers (*Charadrius alexandrinus*), not generally considered colonial but which nest in high density at times, predation at artificial nests in high density areas was greater than in low density areas (Niernuth and Boyce, 1995; Page *et al.*, 1983). These studies used either direct observations of predation attempts or artificial nest experiments, and their demonstration of higher rates of nest loss in colonies tends to be more conclusive than the vast body of literature suggesting reduced predation in colonies, which in most cases infers predation from nesting-success data and cannot rule out other potential effects (see Section 5.3.3).

Higher rates of predation in colonies do not necessarily mean that



individuals there have higher risk. The dilution effect can work as long as predation rates are proportionately lower than individuals could expect as solitaires (Inman and Krebs, 1987; Turner and Pitcher, 1986). This depends on colony size and the absolute predation rate. Relatively little information on actual risk in colonial birds is available: The only quantitative data we are aware of comes from our studies of Cliff Swallows, which show that predation rates (from avian predators and snakes) are proportionately higher in larger colonies, leading to greater per-capita risk for swallows in the largest colonies (Brown and Brown, 1996). In contrast, in *Metepeira incrasata* spiders, which also show higher absolute rates of predation in larger colonies, individual risk declines with colony size because predation rates in large colonies are proportionately lower than in small colonies (Uetz and Hieber, 1994). We are not aware of formal analyses like those of Uetz and Hieber in birds.

## 6. SOCIAL FORAGING AND COLONIALITY

Another potential benefit of avian coloniality is increased foraging efficiency. This can occur in a number of ways: when colony residents use other colony members at the colony site to gain information on the whereabouts of food; when colonial nesting facilitates social foraging away from the colony site; or when birds center their nests in their foraging arenas so as to reduce travel time to and from their nests and food sources. Foraging-related advantages can be expected whenever colonial birds exploit ephemeral and unpredictable food sources, which seems to be the case for most species for which we have data. By far the most widely cited foraging advantage of coloniality is that birds nesting in groups might use each other to increase their rate of food-finding by relying on information from conspecifics that is available at the colony site. This idea can be traced back to Ward's (1965) study of highly gregarious Red-billed Quelea (*Quelea quelea*) in which he observed individuals following others from a communal roost. Independently, Horn (1968) reported that Brewer's Blackbirds sometimes followed owners of neighboring nests to ephemeral food sources and thus found food more rapidly. Soon thereafter, Ward and Zahavi (1973) formally proposed the information-center hypothesis. Intuitively appealing, at least initially, it tended to focus much of the empirical work on coloniality for the next 15 years on this potential mechanism of food finding. Only recently have alternative ways in which colonial birds might improve their foraging efficiency been seriously considered. Although we suffer from a lack of comprehensive studies of foraging in colonial

species, the available evidence is beginning to suggest that social feeding is a strong correlate of avian coloniality and may play a major role in its evolution. As with other effects of coloniality, however, social foraging also may be costly: Colonial birds can potentially deplete food sources near a colony and thus increase the efforts of its members to find food.

This chapter does not deal at length with Horn's (1968) geometrical model for the evolution of coloniality. Horn showed that when food is spatiotemporally variable within a given foraging arena, individuals may minimize their travel distances from the nest site to food by situating their nest in the geometrical center of their foraging arena. Under such conditions, dispersed nesting requires a 31% increase in average distance traveled to find food. A colony forms as each individual attempts to put its nest in the center of the arena, and coloniality may result in the absence of any other benefits of grouping (such as predator avoidance or information sharing). Although a popular explanation for the evolution of coloniality (Wittenberger and Dollinger, 1984), few data exist to evaluate either the model's assumptions or predictions (Brown *et al.*, 1992).

The assumptions inherent in Horn's (1968) model probably present the most difficulty. For example, a foraging arena must be bounded by topographic features or other environmental factors that externally constrain foraging to a given arena; otherwise the advantage of using a centrally located site disappears (Wittenberger and Hunt, 1985; Wittenberger, 1981; Waser and Wiley, 1980). If food is found over a wide, continuous area, birds may form smaller separate colonies or nest solitarily at regular intervals throughout the habitat. Horn's model also implicitly assumes that individuals have the choice to nest either dispersed uniformly throughout the foraging arena or together at a central site. If, however, nesting sites are restricted within the observed foraging arena, individuals are constrained to nest in particular places, which may or may not be the site that minimizes travel distance. For the Cliff Swallow, the only colonial species to which Horn's model has been formally applied, we found that the birds' foraging arenas met neither of the inherent assumptions and therefore the model cannot explain the evolution of colonial nesting (Brown *et al.*, 1992). Because these assumptions are unlikely to hold for most natural populations, the geometrical model is probably a red herring for studies of coloniality.

### 6.1. The Information-Center Hypothesis

The hypothesis that colonial birds improve their foraging efficiency by following other members of the colony to food sparked extensive

work by both field workers and theoreticians and remained viable for a surprisingly long time despite few data to support it. For a colony to serve as an information center and for residents to benefit from it, the following conditions must hold:

1. The food is patchily distributed in space and/or shows ephemeral occurrence in time. This creates a need for information about its location and time of occurrence. A larger number of birds will then have a higher chance to detect a food source.
2. Food patches are rich in order to reduce competition within the patch.
3. The duration of a food patch allows at least one return trip to the colony and back to the patch.
4. Successful foragers return to the colony after having located and exploited a food patch.
5. The colony members can distinguish between successful and unsuccessful foragers. The discrimination is possible on the basis of the feeding success achieved on the immediately preceding foraging trip.
6. After a visit to the colony, the successful foragers return to the previously discovered feeding site.
7. Differences in foraging success between individuals arise by chance in the localization of food or by differing abilities to localize food, not as a consequence of competitive ability or differences in exploitation rates.
8. Unsuccessful foragers that follow others are more successful on their next feeding excursion than unsuccessful foragers that do not follow. (Richner and Heeb, 1995, pp. 4-5)

Early studies of foraging in colonial birds (e.g., Erwin, 1978; Emlen and Demong, 1975; Krebs, 1974) tended not to recognize explicitly or to collect data on these conditions, and consequently did not provide critical tests of the information-center hypothesis. Bayer (1982) showed that many observations regarded as evidence for information centers (such as synchronized departures and arrivals at a colony) were inconclusive and open to other interpretations. At about the same time, the first of several theoretical explorations of information centers appeared with Waltz's (1982) treatment of resource characteristics that favor this sort of information exchange, followed by Beauchamp and Lefebvre (1988), Allchin (1992), and Barta and Szep (1995, 1992). These studies showed information transfer at a colony site via Ward and Zahavi's (1973) mechanism theoretically is likely and may even be the best foraging strategy when, in general, food is clumped, varying in time, and of relatively high abundance in each patch.

Empirical studies, however, have been less supportive. Among colonial nesting birds, only studies of Cliff Swallows (Brown, 1986), Ospreys (*Pandion haliaetus*; Greene, 1987), Common Terns (*Sterna*

*hirundo*; Waltz, 1987), and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*; Gori, 1988) have provided data consistent with the information-center hypothesis, and aspects of all of these studies have been questioned (Richner and Heeb, 1995; Mock *et al.*, 1988). In particular, Mock *et al.* (1988) suggested that all reports of information centers could be explained more parsimoniously by solo foraging or local enhancement in which colony residents observe feeding conspecifics on the foraging grounds and learn the whereabouts of food in that way. Attempted tests of the information-center hypothesis with communally roosting birds in the nonbreeding season have also in general not supported the hypothesis (reviewed in Richner and Heeb, 1995; Mock *et al.*, 1988).

In a detailed critique of the information-center idea, Richner and Heeb (1995) focused on what they regarded as a logical flaw. If colonial birds gain nothing else from nesting with conspecifics, a successful bird does not benefit by traveling back to the colony (or roost) and paying the time and energy costs of travel. Individuals should only return when they have been unsuccessful, which should lead to collections of unsuccessful birds at the colony with no one to follow. A successful bird's voluntary return to the colony and its later providing of information (perhaps unintentionally) to conspecifics who follow it can rightly be regarded as group selection and thus unlikely to evolve (Richner and Heeb, 1995). This problem is most serious if the information center is posited as the only reason birds formed colonies to begin with, because in the initial stages of aggregation, successful birds would have no incentive to return to the colony. Later, after eggs have hatched and nestlings are being fed, individuals must of course regularly return to a fixed site, and at that time the colony could plausibly act as an information center. In this case, the foraging success of some birds could simply be parasitized by others. But if this happens, some other selective force must have originally caused coloniality (see Weatherhead, 1983).

We agree generally with Richner and Heeb's (1995) criticisms of the information-center hypothesis and suggest that ornithologists abandon it as an explanation for the origin (cause) of avian coloniality. However, it still seems likely that information exchange at the colony can occur, as the theoretical studies suggest (Barta and Szep, 1995, 1992; Allchin, 1992; Beauchamp and Lefebvre, 1988; Waltz, 1982), as a consequence of grouping and that the enhanced foraging efficiency that results could affect the overall fitness balance of coloniality (see Section 5). Thus, is there evidence that any colonial bird regularly forages in a manner consistent with the information-center hypothesis?

The best example appears to be that of the Cliff Swallow, which has

also been studied the most extensively (Brown and Brown, 1996; Brown, 1986). Conditions 1–6 (above; Richner and Heeb, 1995) have been verified for Cliff Swallows; no data are available on conditions 7–8. When feeding young, individuals regularly follow colony members to food sources and thereby improve their foraging efficiency. Most important, Cliff Swallows in large colonies have greater foraging success than ones in small colonies, apparently because they waste less time searching. Cliff Swallows are the only colonially nesting bird in which information exchange (through either an information center or other means; Section 6.2) has been studied in relation to colony size (Brown and Brown, 1996). Similar studies on other species are obviously needed.

## 6.2. The Recruitment-Center Hypothesis

As an alternative to the classical information-center hypothesis, Richner and Heeb (1996, 1995) proposed that bird colonies might serve as “recruitment centers” where successful foragers could essentially recruit other foragers to join them at food sources. The assumption is that even birds who are knowledgeable about the whereabouts of food will benefit from feeding in a group, and this benefit will compensate them for the costs of returning to the colony and sharing their information with others. Those who are unsuccessful benefit in much the same way as in an information center, namely, they learn where food is. The birds may act much as they do in an information center, with unsuccessful individuals following others to food, but the recruitment-center hypothesis requires no group selection and is firmly based on the costs and benefits to each individual involved (Richner and Heeb, 1996, 1995). Most important, it also can explain the origin of coloniality in the absence of other potential benefits.

The essence of the recruitment-center hypothesis was proposed first by Evans (1982). His study of Black-billed Gulls (*Larus bulleri*) showed that individuals frequently gave calls upon leaving the colony, and these calls attracted other gulls which followed the callers. Evans (1982) suggested that Black-billed Gulls benefit from group foraging away from the colony, most likely through local enhancement, and for this reason foraging birds recruit others. He anticipated some of Richner and Heeb's (1995) criticisms of the information-center idea, especially its inability to explain initial aggregation. Evans proposed that colonies might instead be advantageous as “assembly points” for group foraging.

All the conditions that define information centers must also hold for recruitment centers (with the possible exception of condition 7; Section 6.1). In addition, if colonies serve as recruitment centers, it is

necessary to show that group feeding away from the colony is beneficial in some way, especially for individuals who already know the location of food. These benefits could be antipredator in nature (improved vigilance, dilution of risk; Section 5.3) or could be because a group increases foraging success through flushing, cooperative hunting, or easier tracking of mobile prey. The recruitment function of colonies can be enhanced when knowledgeable birds give vocal or visual signals to indicate their success (Richner and Heeb, 1996; Evans, 1982). However, although some species may occasionally do this, active signals are not necessary. If successful birds are routinely followed by virtue of their appearance (full crops, food in mouth, direct flight outward), as has been described for some species (Brown and Brown, 1996; Gori, 1988; Waltz, 1987; Brown, 1986), they will reap the benefits of a recruitment center without displaying (and see Zahavi, 1996).

In part because most research has been directed almost exclusively at the information-center hypothesis (Richner and Heeb, 1995), there are virtually no empirical data on recruitment-center mechanisms in colonial birds or how common this behavior may be. However, species that give “recruitment calls” at the colony sites would seem to be good candidates for recruitment centers. In addition to Black-billed Gulls, foraging Ring-billed Gulls (*Larus delawarensis*) departing from colonies give calls (Evans and Welham, 1985). Colonially nesting Ospreys give a particular visual display when returning to their nest sites, which may work to recruit conspecifics to certain, patchily distributed food sources; the display is not given when a bird has been foraging on prey that do not occur in groups and cannot be located again (Greene, 1987). Cliff Swallows have a rarely used “bugs” call (Stoddard, 1988) given at the colony that seems to cause colony members to fly out toward foraging areas. Observations on colonial birds at their feeding grounds and data on how they might benefit from social foraging (and thus recruitment) are even more sparse. Sandwich Terns (*Sterna sandwicensis*; Gochfeld and Burger, 1982) and Black-headed Gulls (Gotmark *et al.*, 1986) are known to use local enhancement to find food on the foraging grounds, probably enhancing their rate of prey capture. In Black-headed Gulls, birds that nest near each other in a colony also tend to maintain feeding associations away from the colony (Prevot-Julliard and Lebreton, 1999), consistent with recruitment of neighbors to foraging sites.

The most thorough work on foraging of a colonial species away from its colony sites has been done on Cliff Swallows. This species often feeds in groups, and individuals foraging in groups average more prey captures per minute than solitary foragers (Brown, 1988). Variance in prey captures also declines with foraging group size. These advantages

seem to stem mostly from more efficient tracking and discovery of ephemeral insect swarms that often appear and disappear on localized convection currents (Brown and Brown, 1996). Cliff Swallows also use local enhancement on their foraging grounds and converge on birds that have located insects (Brown, 1988). Swarms of insects appear to be so dense that no significant depletion of a food patch occurs regardless of the number of birds foraging there. Cliff Swallows actively benefit from social foraging in part because the presence of more birds ensures that the highly mobile and spatially variable insect swarms can be more continually tracked (Brown *et al.*, 1991). Thus by feeding in a group, a given forager will be more likely to relocate the swarm later, perhaps after it makes a trip back to the colony to deliver food to nestlings. Consistent with this, Cliff Swallows give specific food calls on the foraging grounds after finding a swarm, recruiting conspecifics to feed there (Brown *et al.*, 1991). Food calls are seemingly confined to periods of bad weather when insect swarms are particularly difficult to find and perhaps when it is more critical to keep track of those that are found.

### 6.3. Spatial Concentration and Local Enhancement

A recent study by Buckley (1997) provides additional support for the view that foraging advantages away from the colony site may select for colonial nesting in birds. Buckley's work was intended to address primarily coloniality in seabirds, but it is potentially applicable to any species. He assumed that colonial birds often use local enhancement to find prey, an assumption that seems to hold at least for gulls and swallows (see Section 6.2). Coloniality may be advantageous because it simply concentrates potential foragers in space, allowing the birds to find food more effectively through local enhancement mechanisms. If a food source is large and short-lived, yet also patchily distributed, local enhancement will be the most effective way to locate it. This happens because feeding flocks are more conspicuous than the food itself, and the area of effective search (the combined region searched by multiple foragers) will be much larger than the area a single bird can search. Abundant food ameliorates the negative consequences of sharing food with others and makes social foraging advantageous; if food is exhaustible within patches, social feeding does not increase food-intake rates (Beauchamp, 1998; Ruxton *et al.*, 1995). When Buckley (1997) simulated food of different degrees of patchiness and abundance at different distances from a colony site, he found, as Horn (1968) first suggested, that colonial nesting would lead to more efficient rates of food discovery than dispersed nesting when food was patchy and abundant within

each patch. Dispersed nesting is favored if food is found in small, long-lived patches. Buckley's results seem to indicate that under the right circumstances, individuals playing a colonial strategy can invade a population of solitary nesters, whereas coloniality, once established, is resistant to invasion by solitary nesters.

That solitary nesting birds could also use local enhancement to find food has been argued (Hoogland and Sherman, 1976), and coloniality does not necessarily have to evolve for birds to find patchily distributed food. In theory, solitary nesters could commute to a common foraging area where they could benefit from local-enhancement effects. Their ability to do this will depend at least on how far they nest from the foraging area and how dispersed their nests are. Buckley's (1997) work is the first to model quantitatively the degree to which solitary foragers could use local enhancement and whether they could get the same advantage as colonial nesters. His simulations show that when prey is patchy and ephemeral, solitary nesters cannot gain the same advantage colonial nesters have, at least under the conditions of the model (Buckley, 1997). In short, coloniality spatially concentrates foragers so that local enhancement and other benefits of group foraging (risk aversion, antipredator effects) can operate, and they do so more efficiently than they would for dispersed nesters. The same argument was made by Krebs (1978, 1974), Brown (1988), and Brown *et al.* (1991). Buckley's analyses (1997) also show that colonies can grow to large size when ecological conditions are suitable, and local-enhancement advantages provide an incentive for this growth. His study is particularly interesting, because it is one of the few formal evolutionary analyses of coloniality using game theory. Buckley (1997) concluded that spatial concentration effects have probably led to coloniality in many seabirds, which is consistent with Rolland *et al.*'s (1998) phylogenetic analyses showing exploitation of patchily distributed food strongly linked to coloniality.

Spatial-concentration effects and local enhancement do not require colonies to serve as recruitment centers; colonial birds could reap foraging-related advantages solely as a consequence of a concentrated number of foragers in the vicinity of the colony without active recruitment of foragers to the feeding areas. But if colonies serve as recruitment centers, the advantages described by Buckley (1997) may be enhanced. The common threads through both spatial-concentration effects and recruitment centers are a patchy, concentrated, and short-lived food source and the benefits of foraging socially on the feeding grounds. At least with respect to the characteristics of the food source, it appears that many, if not most, colonial species use food resources distributed in this

way (Brown and Brown, 1996; Clode, 1993; Kopachena, 1991; Wittenberger and Hunt, 1985).

#### 6.4. Competition and Depletion of Food

One possible consequence of coloniality is competition for food among colony members and the resultant depletion of local food resources. This might be most likely in extremely large colonies, where greater demands are placed on local resources. This is especially true when young hatch and parents must harvest food virtually continuously. If food competition is severe, it can be another cost of coloniality and may negate foraging-related advantages that come from information transfer and group feeding (see Sections 6.1–6.3).

The view that bird colonies may deplete food resources near the colony site was first presented by Ashmole (1963), who proposed that seabird colonies often are surrounded by a region (a "halo") where prey has been depleted as a result of the foraging activities of colony members. As the halo develops, colony members must fly to increasingly distant waters to forage. In their review of avian coloniality, Wittenberger and Hunt (1985) viewed food competition and resource depletion as a negative consequence of colonial nesting for most species.

However, few direct data on actual food availability around colonies exist, for either seabirds or other colonial birds (Brown and Brown, 1996; Hunt *et al.*, 1986). Sampling food sources is difficult for most species, either because of the great diversity of food sources used and the different sampling methods required for each, or because of the spatial scale over which foraging occurs. In Cliff Swallows, dozens of insect taxa are taken by the birds, and each requires a sampling method tailored to its natural history (Brown and Brown, 1996; Cooper and Whitmore, 1990). Most seabirds feed over such enormous expanses of water that meaningful sampling of food is virtually impossible (Hunt and Schneider, 1987). The few attempts to sample food of terrestrial colonial birds either were done for a single site only (Bryant, 1975) or sampled insects by only one method and were thus probably biased in unknown ways (Earle and Underhill, 1991; Møller, 1987). A perhaps more conclusive approach was used by Birt *et al.* (1987), in which scuba divers counted fish along transects near Double-crested Cormorant (*Phalacrocorax auritus*) colonies. They found that fish were less abundant in bays used by cormorants for foraging than in bays not used, providing probably the only direct support for Ashmole's (1963) halo hypothesis. In contrast, direct observations of foraging Cliff Swallows found no differences in the number of prey captures per minute in

groups of different sizes, implying no competition for food as colony size (and thus foraging group size) increased (Brown and Brown, 1996).

Perhaps because of the problems inherent in direct sampling of food sources, most studies have inferred the presence or absence of competition for food from indirect measures of chick growth rates, chick starvation rates, feeding rates, fledging mass, correlations between colony sizes and total number of foragers in an area, mass abandonments of sites, travel distances, and total colony foraging area (Griffin and Thomas, 2000; Beauchamp, 1999a; Brown and Brown, 1996; Ainley *et al.*, 1995; Cairns, 1992; Hunt *et al.*, 1986; Wittenberger and Hunt, 1985; Furness and Birkhead, 1984; Gaston *et al.*, 1983; Orians, 1961). In seabirds, these measures of foraging success often have suggested that birds find less food in larger colonies; this was termed the "hungry horde" effect (Cairns, 1992). If so, this indicates that factors other than enhanced foraging efficiency cause seabirds to form colonies. A number of explanations, none of which seems particularly compelling, have been advanced to account for this pattern (Cairns, 1992, 1989).

It is not clear that seabirds really deplete their food supplies near a colony. The correlative evidence on growth rates, mass, etc., is in most cases inconclusive, principally because it does not take into account that composition of large and small colonies, and thus the quality of the birds occupying each, may differ substantially (see Section 9). Showing a reduction in fledging mass for birds in large colonies relative to small colonies, for example, does not show food depletion at large sites because young or naive individuals might be more likely to settle in large colonies and the lower mass of their chicks might be because they are inexperienced foragers relative to the older birds in small colonies (Brown and Brown, 1996). The question would be how the same individuals would perform in a small colony, and without experimental changes in colony size, we generally do not know this.

The strongest of the indirect correlative evidence for or against food competition and resource depletion is probably that related to travel distance. It is generally accepted that birds should feed as close as possible to their nest sites and travel the minimum distance necessary to find food (Andersson, 1978; Horn, 1968), and therefore longer travel distances should mean that food is insufficient close to the colony (Furness and Birkhead, 1984; Orians, 1971; Hamilton and Watt, 1970). Presumably both low-quality and high-quality birds should minimize commuting distance, and consequently this measure of relative food availability among sites should be less sensitive to individual performance differences. Although data on primates suggest that daily travel distance increases with group size, probably because of competition for

food (Janson, 1988; van Schaik *et al.*, 1983), there are few similar data for birds. For Cliff Swallows, both average commuting distance traveled from the colony to food patches and a colony's total area over which its residents foraged increased significantly with colony size (Brown and Brown, 1996). This led to the conclusion that Cliff Swallows do deplete insect availability near their colonies and this effect is stronger at larger colonies. Yet overall foraging efficiency remains higher, on average, in the larger colonies because of information transfer, which allows the birds to compensate for food depletion (Brown and Brown, 1996). The net foraging effect of coloniality in Cliff Swallows is positive, but this might not be the case in all species, underscoring the importance of determining whether food depletion is a significant cost. In a study of penguins in the Antarctic, Ainley *et al.* (1995) concluded there was little strong evidence of prey depletion at colonies, and if competition for food occurred, it was overridden by factors that promoted coloniality. The obvious conclusion (*contra* Wittenberger and Hunt, 1985) is that in general we have no idea whether colonially nesting birds compete for food and deplete food sources near their colonies or whether this is an important enough cost to constrain the evolution of coloniality.

## 7. REPRODUCTIVE SUCCESS AND HABITAT SELECTION

The empirical work over the last 25 years shows that a variety of costs and benefits are associated with avian coloniality. The magnitudes of these effects obviously vary among different species and even among different colonies and different individuals of the same species, while some may not apply at all in a particular case. Each affects fitness, often in complex ways that may be density dependent or frequency dependent, and multiple ones may be correlated with each other in nonlinear ways. For example, as social foraging increases, so does the potential for competition for food, and thus the benefit of quicker food discovery may covary in an unknown fashion with the likelihood of food depletion. In the best studied case, the Cliff Swallow, we were generally unable to specify the exact effect that each cost or benefit of coloniality had on fitness (Brown and Brown, 1996).

These difficulties have led to implicit calls to abandon the "economic" approach of measuring costs and benefits (the paradigm on which much of modern behavioral ecology is based) and instead focus on how coloniality might be explained by proximate mechanisms of habitat choice (Wagner *et al.*, 2000; Danchin and Wagner, 1999, 1997). The key idea essentially is that breeding habitat is heterogeneous, and some sites are better for nesting than others. By observing the reproduc-

tive success of current breeders at various sites, failed breeders and nonbreeders use that information to choose (perhaps the next season) those sites where reproductive success had been highest. An aggregation (a colony) forms at the sites with favorable conditions (Danchin *et al.*, 1998; Boulinier and Danchin, 1997; Forbes and Kaiser, 1994). Promoted as a new paradigm for studies of coloniality (Danchin and Wagner, 1999), this approach is useful for predicting patterns of colony growth or decline. However, it does not explain what causes success at some breeding sites to be better than others or why aggregations at favorable sites occur in some species but not in others. Knowing the cause(s) of greater success at some sites requires measurement of the ecological and social factors that influence reproductive success in colonies of different sizes, the traditional cost-benefit approach. Nevertheless, Danchin and Wagner's (1999, 1997) emphasis on reproductive success in studies of coloniality is long overdue.

Reproductive success has been studied in colonial birds by analyzing the mean success among all individuals in the colony and then comparing means among colonies, and by focusing on the variability in reproductive success among individuals within a colony (e.g., those nesting in the center versus the edge). Mean reproductive success reveals how individuals, on average, can expect to perform in colonies of a given size. It is important to recognize, however, that colonies consist of individuals that often differ considerably in their inherent abilities (Brown and Brown, 1996; Section 9), and within a colony there may be significant spatial or temporal heterogeneities that may influence an individual's expectation of success (Danchin *et al.*, 1998).

### 7.1. Mean Reproductive Success in Relation to Colony Size

Any evolutionary analysis of behavior ultimately seeks to understand how fitness is affected by variation in that behavior. In studying coloniality, ornithologists are often interested in measuring the net effect on fitness of different colony sizes or habitat patches. Reproductive success, measured either seasonally or (more rarely) over an individual's entire lifetime, is the best measure of fitness available in natural populations (Newton, 1989; Partridge, 1989; Grafen, 1988). By reflecting the sum total of both positive and negative consequences of aggregation, mean reproductive success can reveal whether individuals suffer a net cost or net benefit and which, if any, group sizes or habitat patches are best (Brown and Brown, 1999b, 1996). The pattern in reproductive success can be informative. An increase in mean reproductive success with colony size shows a net advantage to coloniality and thus that individuals on average probably benefit from the presence of conspecifics in



some way, perhaps through predator avoidance or more efficient food finding. In contrast, a decrease in mean reproductive success with colony size shows a net cost to coloniality and thus that animals are probably forced into colonies by limited breeding habitat or other constraints (Brown and Brown, 1996; Brown *et al.*, 1990). Besides being useful to researchers, information on reproductive success may also be important to the animals themselves as they choose where to settle (see Section 7.2).

Several field studies have measured the reproductive success of colonial birds in relation to colony size or in colonies versus solitary nests (Table I). The strongest studies are those whose primary objective was to measure the effect of colony size on reproductive success and used each colony (not each nest) as an independent sampling unit (e.g., Davis and Brown, 1999; Huhta, 1999; Brown and Brown, 1996; Butler *et al.*, 1995; Jehl, 1994; Wiklund and Andersson, 1994; van Vesseem and Draulans, 1986; Gotmark and Andersson, 1984). Many of those with relevant data, though, were done with other objectives, and over 60% based their conclusions on fewer than 10 colonies (Table I). Studies have commonly pooled multiple colonies into a single "colonial" category or a smaller number of colony-size classes, diminishing their ability to test rigorously for an effect of group size. Those studies with sample sizes less than ten have low statistical power and must be treated cautiously. Interestingly, the pattern seems to be for studies reporting an effect of colony size to be slightly more likely to have had a relatively small sample of colonies or colony-size classes (Table I); in some of these, the effects would undoubtedly vanish with a finer scale comparison across a wider range of colony sizes. Those finding no effect of colony size or an intermediate optimum are more likely to be based on a larger number of colonies and may be more reliable (Table I).

This tabulation does not include the scores of studies that measured reproductive success in relation to nest density at what was reported to be a single colony. Some of the nest-density studies may have included comparisons among functionally different colonies, as a common practice has been to designate certain parts of a "colony" (on an island, for example) based on different nest densities and to test for differences among them. The degree of contact between these subgroups of birds at the same site is usually not reported, however, illustrating the difficulties in defining a "colony" in some species and forcing us to exclude some studies with potential information.

With these limitations in mind, the available evidence suggests the two most common patterns are an increase in mean reproductive success with colony size (27 studies) and no effect of colony size on repro-

ductive success (25 studies; Table I). Most of the studies reporting an increase in mean reproductive success with colony size (Table I) attributed the greater success in larger colonies to better avoidance of predators. However, as pointed out earlier (see Section 5.3), few have clearly demonstrated that predators are avoided more effectively in groups and that higher reproductive success is not simply because higher-quality birds settle in the larger colonies. Still, these studies suggest that individuals probably benefit in some substantive way from associating with conspecifics while breeding. Exceptions do occur: In Huhta's (1999) study of Bank Swallows, she found that larger colonies formed in areas with more compact soil, and the compact soil resulted in fewer burrow collapses. Yet it was the soil, not colony size per se or associations with conspecifics, that led to higher reproductive success in larger colonies. Increased success in larger groups also demonstrates an "Allee effect," in which individuals at low density are not as effective at foraging, finding mates, or avoiding predators (Courchamp *et al.*, 1999; Stephens and Sutherland, 1999).

It is unclear what is the nature of the benefits, if any, that individuals derive from coloniality in those species (Table I) in which there is no apparent difference in mean reproductive success among group sizes. In cases like the Purple Martin, colonies in general do not seem to reach large enough sizes for either benefits (predator avoidance, social foraging) or costs of coloniality (ectoparasitism, competition for resources and mates) to be substantive, and thus we see no strong effect of colony size on reproductive success (Davis and Brown, 1999). In other cases, both costs and benefits may be substantial in larger groups, but their effects on fitness balance each other, leading to no difference in average reproductive success between large and small colonies; this appears to be true in some years for the Cliff Swallow (Brown and Brown, 1996).

A few studies have shown a decrease in mean reproductive success with colony size (Table I). This pattern has traditionally been viewed as strong evidence that coloniality is on average disadvantageous with costs exceeding benefits (Brown and Brown, 1996; Shields and Crook, 1987), and it seems to suggest that individuals would prefer to nest solitarily but must be forced into colonies by lack of suitable nesting sites. An alternative interpretation is that low-quality birds settle in the larger colonies and reproduce less well simply because of their inherent abilities. For example, in Cliff Swallows, older, heavier birds that are less parasitized by fleas tend to settle in smaller colonies (Section 9.2; Brown and Brown, 1996), and this complicates the interpretation of differences in mean reproductive success between colonies in this species.



TABLE I

Studies on Colonial Birds Reporting How Reproductive Success Varies with Colony Size (Includes Comparisons of Solitary Nests with Colonial Nests)

Species	N	Source
A. Reproductive Success Increases with Increasing Colony Size		
Gentoo Penguin ( <i>Pygoscelis papua</i> )	6	Robertson, 1986
Northern Fulmar ( <i>Fulmarus glacialis</i> )	3	Fisher and Waterston, 1941
Northern Gannet ( <i>Morus bassanus</i> )	? (5)	Fisher and Vevers, 1944
Northern Gannet	?	Nelson, 1978
Black Brant ( <i>Branta bernicla</i> )	4	Raveling, 1989
Least Bittern ( <i>Ixobrychus exilis</i> )	8 (25)	Post and Seals, 1993
Glossy Ibis ( <i>Plegadis falcinellus</i> )	2	Miller and Burger, 1978
Lesser Kestrel ( <i>Falco naumanni</i> )	109 (68)	Tella, 1996
Mew Gull ( <i>Larus canus</i> )	23 (13)	Gotmark and Andersson, 1984
Audouin's Gull ( <i>Larus audouinii</i> )	2	Oro <i>et al.</i> , 1996
Herring Gull ( <i>Larus argentatus</i> )	8	Burger, 1979
Black-headed Gull ( <i>Larus ridibundus</i> )	1 (125)	Patterson, 1965
Common Tern ( <i>Sterna hirundo</i> )	5	Morris and Hunter, 1976
Common Tern	4	Burger and Gochfeld, 1991
Gull-billed Tern ( <i>Sterna nilotica</i> )	2	Møller, 1981
Sandwich Tern ( <i>Sterna sandvicensis</i> )	12	Veen, 1997
Black Skimmer ( <i>Rynchops niger</i> )	14	Burger and Gochfeld, 1990
Common Murres ( <i>Uria aalge</i> )	3	Birkhead, 1977
Eurasian Jackdaw ( <i>Corvus monedula</i> )	3	Johnsson, 1994
Fieldfare ( <i>Turdus pilaris</i> )	13 (14)	Wiklund and Andersson, 1980
Fieldfare	5 (37)	Haas, 1985
Bank Swallow ( <i>Riparia riparia</i> )	12	Huhta, 1999
Cliff Swallow ( <i>Petrochelidon pyrrhonota</i> )	8	Brown and Brown, 1996
Eurasian Tree Sparrow ( <i>Passer montanus</i> )	5 (~125)	Sasvari and Hegyi, 1994
Yellow-rumped Cuckoo ( <i>Cacicus cela</i> )	? (190)	Robinson, 1985
Red-winged Blackbird ( <i>Agelaius phoeniceus</i> )	9	Robertson, 1973
Tricolored Blackbird ( <i>Agelaius tricolor</i> )	?	Orians, 1961
B. Reproductive Success Decreases with Increasing Colony Size		
Common Shelduck ( <i>Tadorna tadorna</i> )	3 (24)	Pienkowski and Evans, 1982
Brown-hooded Gull ( <i>Larus maculipennis</i> )	6 (16)	Burger, 1974
Black-legged Kittiwake ( <i>Rissa tridactyla</i> )	13	Birkhead and Furness, 1985
Black-legged Kittiwake	9	Hunt <i>et al.</i> , 1986
Atlantic Puffin ( <i>Fratercula arctica</i> )	2	Nettleship, 1972
Least Tern ( <i>Sterna antillarum</i> )	2	Burger, 1984
Fieldfare ( <i>Turdus pilaris</i> )	1 (47)	Haas, 1985
Barn Swallow ( <i>Hirundo rustica</i> )	4	Shields and Crook, 1987
Eurasian Tree Sparrow ( <i>Passer montanus</i> )	1 (~125)	Sasvari and Hegyi, 1994

TABLE I (Continued)

Species	N	Source
C. No Relationship Between Reproductive Success and Colony Size		
Eared Grebe ( <i>Podiceps nigricollis</i> )	4	Hill <i>et al.</i> , 1997
Red-faced Cormorant ( <i>Phalacrocorax urile</i> )	2	Hunt <i>et al.</i> , 1986
American White Pelican ( <i>Pelecanus erythrorhynchos</i> )	35	Knopf, 1979
Grey Heron ( <i>Ardea cinerea</i> )	10	van Vessem and Draulans, 1986
Great Blue Heron ( <i>Ardea herodias</i> )	5	Werschul <i>et al.</i> , 1977
Great Blue Heron	31	Butler <i>et al.</i> , 1995
Buff-necked Ibis ( <i>Theristicus caudatus</i> )	11	Donazar <i>et al.</i> , 1994
Snail Kite ( <i>Rostrhamus sociabilis</i> )	2 (141)	Snyder <i>et al.</i> , 1989
California Gull ( <i>Larus californicus</i> )	10	Jehl, 1994
Herring Gull ( <i>Larus argentatus</i> )	4	Darling, 1938
Herring Gull	3	Burger and Shisler, 1978
Herring Gull	9	Kilpi, 1995b
Red-legged Kittiwake ( <i>Rissa brevirostris</i> )	2	Hunt <i>et al.</i> , 1986
Little Tern ( <i>Sterna albigrons</i> )	5	Holloway, 1993
Common Murre ( <i>Uria aalge</i> )	5	Hunt <i>et al.</i> , 1986
Thick-billed Murre ( <i>Uria lomvia</i> )	6	Hunt <i>et al.</i> , 1986
Fieldfare ( <i>Turdus pilaris</i> )	6 (116)	Hogstad, 1983
Fieldfare	5	Haas, 1985
Bearded Tit ( <i>Panurus biarmicus</i> )	1 (30)	Hoi and Hoi-Leitner, 1997
Purple Martin ( <i>Progne subis</i> )	13	Davis and Brown, 1999
Bank Swallow ( <i>Riparia riparia</i> )	46	Hoogland and Sherman, 1976
Cliff Swallow ( <i>Petrochelidon pyrrhonota</i> )	19	Brown and Brown, 1996
Barn Swallow ( <i>Hirundo rustica</i> )	5	Snapp, 1976
Red-winged Blackbird ( <i>Agelaius phoeniceus</i> )	3	Smith, 1943
Boat-tailed Grackle ( <i>Quiscalus major</i> )	7	Post, 1994
D. Reproductive Success Peaks at Intermediate Colony Size		
Least Tern ( <i>Sterna antillarum</i> )	11	Brunton, 1999
Cliff Swallow ( <i>Petrochelidon pyrrhonota</i> )	17	Brown and Brown, 1996
Fieldfare ( <i>Turdus pilaris</i> )	106 (86)	Wiklund and Andersson, 1994

N: number of independent colonies or pooled colony-size classes on which result was based, unless unreported or unclear (denoted with ?); sample size for solitary nests shown in parentheses.

Perhaps the most interesting pattern is that in which mean reproductive success peaks at an intermediate colony size (Table I). Few studies have shown this, possibly because it is difficult to demonstrate curvilinear trends with small sample sizes. In these species an optimal colony size may exist, one in which the net difference between benefits

and costs is greatest. It is easy to visualize a situation where, say, the cost of ectoparasitism becomes prohibitive at large colonies, whereas the benefit of social foraging increases with colony size up to a certain size, at which point travel distance and harvest time considerations negate any further increase in the advantage associated with increasing group size. Because the cost of coloniality continues to increase, colonies larger than some threshold size should not occur. When the benefits and costs of coloniality vary nonlinearly in relation to group size, intermediate colony sizes where fitness is predicted to be highest will occur; the shape of the curves and thus the optimal colony size may differ among individuals within a population (Figure 1; Burger, 1981, Section 9.2). The same idea has been applied to analyzing territory size in birds (Wittenberger, 1981).

The strongest empirical data suggesting optimal colony sizes (Table 1) come from studies of Fieldfares, in which increased chick starvation in large colonies and increased predation in small colonies led to highest success in colonies of medium size (Wiklund and Andersson, 1994; Wiklund, 1982). In some years, mean reproductive success in Cliff Swallows peaks at intermediate-sized colonies, brought about by a complex interplay of colony size-dependent costs and benefits that also may vary

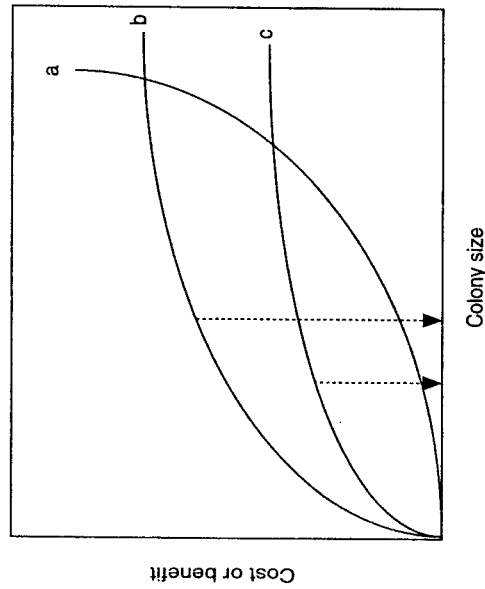


FIGURE 1. Hypothetical cost and benefit of coloniality in relation to colony size for two individuals of different phenotypes. The cost (a) is the same for all birds, but the benefits (b, c) differ depending on phenotypic characteristics. For each phenotype, the point of maximum net positive difference between benefit and cost (dashed line) represents the optimal colony size.

by year (Brown and Brown, 1996). Predation by different kinds of predators appears to favor intermediate-sized colonies in Least Terns (Brunton, 1999). Small tern colonies are heavily preyed upon by mammals, gulls, and crows, and large colonies are often attacked by Black-crowned Night Herons; intermediate-sized colonies have the lowest rates of predation by each type of predator. In Herring Gulls (*Larus argentatus*), birds that nest at intermediate nest densities within colonies have the highest success, apparently brought about by young and inexperienced individuals occupying low-density areas and high rates of cannibalism from conspecifics in the high-density areas (Parsons, 1976). Nests at intermediate densities within a Magellanic Penguin colony also had highest success, for unknown reasons (Scolaro, 1990).

There is obviously no general conclusion that can be made from the body of literature on mean reproductive success in colonial birds (Table 1). Some species show different patterns in the same population in different years (e.g., Cliff Swallows), among different broods in the same year (e.g., Eurasian Tree Sparrows [*Passer montanus*], Fieldfares; Sasaki and Hegyi, 1994; Haas, 1985), or among different geographic areas (e.g., Fieldfares in Sweden versus Norway; Hogstad, 1983; Wiklund and Andersson, 1980). A ten-year study of California Gulls (*Larus californicus*) found no significant relationship between colony density (size) at a single site and annual fledging success. However, had only the first six years been included in the study, fledging success would have decreased significantly with colony size; had only the last seven years been included, fledging success would have increased significantly (Jehl, 1994)!

These different patterns between and within species may reflect real variability and show that different selective pressures do or do not promote coloniality at different times. However, this variation may also reflect in part the limitations of the data and that we have few good estimates of fitness for individuals in groups of different sizes. The available data on reproductive success in colonial birds is primarily that for a single nesting season, or, more precisely, annual fledging success, which may or may not correlate with lifetime reproductive success, especially in long-lived birds (Newton, 1989; Clutton-Brock, 1988; Birkhead and Furness, 1985). No one to date has measured lifetime reproductive success in relation to colony size, mostly because of the difficulties of following individuals that may occupy different breeding sites or not breed at all in some years. These difficulties are compounded because many colonial birds are long-lived (e.g., seabirds) and tend to be migratory or nomadic, not allowing their fates to be monitored in the same way as, for example, sedentary cooperative breeders. This funda-

mental difference between colonial and cooperative-territorial species and its consequences for data collection have contributed in part to a less rich conceptual understanding of coloniality than territoriality or cooperative breeding systems (e.g., see Brown, 1987).

## 7.2. Using Reproductive Success to Select Breeding Sites

Reproductive success helps determine the breeding decisions birds make. For example, it may be used in deciding whether to change mates between breeding attempts (Black, 1996) or whether to disperse to a new nesting site (Part and Gustafson, 1989; Cuthbert, 1988; Greenwood and Harvey, 1982). Colonial birds may also use reproductive success to determine the most suitable sites for breeding. Forbes and Kaiser (1994) and Danchin and Wagner (1997) proposed that coloniality is a consequence of animals assessing habitat on the basis of the success of conspecifics already breeding there and choosing to settle in sites that promote success. This view holds that coloniality is simply a byproduct of habitat selection rules that apply whenever a habitat is heterogeneous and some sites within the habitat are better than others.

The possibility that bird colonies might result from relatively simple decision rules by individuals in a heterogeneous environment can be traced back to at least Shields *et al.* (1988). They proposed that swallows, faced with choosing breeding sites, would use the presence of old nests as an indication that nesting was likely to be successful at a particular site. If a nest survived intact from one year to the next, the site was presumed to be safe. This would lead to clumped distributions of birds at the successful sites (colonies) and gradual abandonment of less successful sites. Shields *et al.* (1988) assumed a site's success is predictable from year to year, and thus colonies tend to occur at the same safe sites each year (traditional aggregations). This hypothesis, like all of those involving habitat selection processes (Wagner *et al.*, 2000; Danchin and Wagner, 1999, 1997; Boulmier and Danchin, 1997; Forbes and Kaiser, 1994), does not address what makes some sites successful and others not, a critical point we discuss later. The model proposed by Shields *et al.* (1988) also predicts formation of a few massive colonies at the successful sites instead of the range in colony sizes seen in most populations (Brown and Rannala, 1995; Brown *et al.*, 1990; Section 9).

There is little evidence that bird colonies in general result from traditional-aggregation processes as described by Shields *et al.* (1988). This process can only apply to species whose nests remain intact from year to year; otherwise, prospective settlers have no way to gauge last year's reproductive success. Some data for Barn Swallows seem to sup-

port this sort of habitat selection (Shields *et al.*, 1988) while others do not (Barclay, 1988). Some night herons and egrets seem to prefer sites with old nests, although their site choice is also based on other factors such as presence of conspecifics (Davis, 1986). Cliff Swallows do not choose colonies in a traditional-aggregation way (Brown and Brown, 1996).

The hypothesis of Forbes and Kaiser (1994) and Danchin and Wagner (1999, 1997) essentially refines that of Shields *et al.* (1988), making some of the same assumptions, yet it proposes direct observation of reproductive success as the cue used by animals to select breeding sites. By visiting occupied nesting sites and observing actual nesting activity, failed breeders and nonbreeders in one year can gain information to help them select nesting sites the next year. This hypothesis is consistent with the presence of "prospectors" in many colonial birds—nonbreeding or postbreeding individuals that circulate among existing colonies, often coming into close proximity to active nests (Bradley *et al.*, 1999; Boulmier *et al.*, 1996; Danchin *et al.*, 1991; Harrington, 1974). Colonies result because the best sites attract more of these prospectors (then breeders) the next year, plus the former residents there are likely to return owing to their past success. Less successful sites attract fewer birds and gradually become vacant. The novel aspect of this hypothesis is that individuals use the reproductive success of others, not their own, to make settlement decisions. Consequently, this process relies on public information to make habitat choices and to some degree is similar to cases in which animals use public information (e.g., local enhancement) to find productive foraging sites or possibly mates (Valone and Benkman, 1999; Dubois *et al.*, 1998; Forbes and Kaiser, 1994). Unlike with the Shields *et al.* (1988) traditional-aggregation hypothesis, settlement based on past reproductive success can apply to species whose nests do not routinely last between seasons.

The critical assumption underlying a habitat selection process based on past success is that breeding sites (habitat "patches") are autocorrelated in their suitability from one year to the next. If not, a "good" site this year may be no more likely to be "good" next year as one chosen at random. When particular patches are traditionally good, colonies will form and be maintained there and perhaps grow through the mechanism advocated by Forbes and Kaiser (1994) and Danchin and Wagner (1997). Furthermore, Forbes and Kaiser (1994) argue that coloniality may be maintained in part by the animals not having information on some potential sites simply because no birds have ever nested there. If birds select sites only on the basis of how previous residents perform, "good" sites that no birds have happened to have used are functionally

unavailable, and this "information barrier" may work to concentrate individuals into the few sites known to be favorable.

If colonial birds select sites based on public information about reproductive success, the following testable predictions are possible (Brown *et al.*, 2000; Valone and Benkman, 1999; Boulinier and Danchin, 1997; Danchin and Wagner, 1997).

1. An individual's decision to move to a new colony site or return to the same colony site the next year should be a function of the average reproductive success of a colony in the current year; philopatry should be high at sites with high reproductive success and low at sites with low reproductive success.
2. An individual changing colony sites between years should move to one that had higher mean reproductive success than the one it used the previous year.
3. Nonbreeders in one year should settle the next year at the colony sites with the highest mean reproductive success the previous year.
4. If colonies differ in mean reproductive success, those with mean reproductive success higher than that within the population as a whole should grow in size because of a net recruitment of breeders.

Few studies of colonial birds have explicitly tested this habitat selection model. Danchin *et al.* (1998) learned that all four predictions held for Black-legged Kittiwakes (*Rissa tridactyla*). They found that the quality of colony sites (measured as mean reproductive success) tended to be autocorrelated over 1–2 year time periods, verifying the assumption that the environment was predictable enough from year to year that information one year would be useful the next. Nonbreeding kittiwakes also commonly prospect for nesting sites by visiting active colonies late in the season as birds are feeding chicks, which is when the best information on reproductive success at a site is available (Boulinier *et al.*, 1999, 1996; Cadiou, 1999). Results for Cliff Swallows also tended to match the predictions and assumptions of a habitat selection model based on assessment of conspecific performance (Brown *et al.*, 2000). Cliff Swallow colonies often vary substantially in size from year to year, and the correlation between the extent of recruitment of new breeders and last year's reproductive success provides strong support for the model. As in kittiwakes, large numbers of nonbreeding Cliff Swallows visit active colonies while nestlings are being fed, apparently to assess breeding performance (Brown, 1998; Brown and Brown, 1996). For the

Buff-necked Ibis (*Theristicus caudatus*), data presented by Donazar *et al.* (1994) were reanalyzed by Boulinier (1996) to show a positive correlation between mean reproductive success in one year and growth of the colony at that site the next year, consistent with the results from kittiwakes and swallows. In the Mew Gull, colonies that had fewer major predation events tended to increase in size from year to year, and those with predation declined in size, broadly consistent with the habitat-selection hypothesis (Kilpi, 1995a). In the Northern Gannet (*Morus bassanus*), successful colonies grew at a faster rate than could be accounted for by local offspring production, suggesting recruitment from outside the colony (Nelson, 1978). In Great Cormorants (*Phalacrocorax carbo*), site fidelity of females was related to the success of neighbors. Apparently, the birds were using conspecific reproductive success to make settlement decisions (Schjørring *et al.*, 2000).

However, in the Audouin's Gull (*Larus audouinii*), reproductive success in the previous year had no effect on the number of first-time breeders settling in a colony; these gulls made settlement decisions based mostly on colony size (Oro and Pradel, 2000). In the Gull-billed Tern (*Sterna nilotica*), mean reproductive success one year had no effect on whether that colony site was used next year (Erwin *et al.*, 1998). Gull-billed Terns seem to show little pattern in their annual use of colony sites, other than to be generally unlikely to use the same colony site for multiple years. A similar pattern was found in Least Terns, which sometimes reoccupy sites that had complete reproductive failure the preceding season (Burger, 1984). Terns and some gulls often occupy highly ephemeral breeding habitat subject to frequent flooding or erosion (Erwin *et al.*, 1998; Burger, 1984; McNicholl, 1975), and thus site suitability from one year to the next apparently varies so much that accurate predictions of relative success cannot be made. Colony sites also are seldom reused the next year in White-fronted Bee-eaters (*Merops bullockoides*; Hegner *et al.*, 1982). This illustrates that even though species as diverse as ibises, kittiwakes, and swallows may choose breeding habitat based on last year's performance of conspecifics, this mechanism of colony formation does not apply to all colonial birds.

The model of habitat selection proposed by Forbes and Kaiser (1994), Danchin and Wagner (1997), and Wagner *et al.* (2000), is strictly a proximate mechanism that says nothing about why certain sites or patches within the habitat are favorable and others are not. Are some colony sites good because of proximity to abundant resources (food, high quality nest sites), or are some sites good because many birds happen to be breeding there and the benefits of information transfer or predator avoidance increase mean reproductive success? One possi-

attract immigrants because of its past low success, and the reduced number of residents does not attract naive yearlings. Thus, in Cliff Swallows, colony choice apparently includes assessment of conspecific breeding performance, attraction to conspecifics, and use of individual reproductive success in making dispersal decisions (Brown *et al.*, 2000). However, to determine what causes the differences in reproductive success among colonies, and ultimately the aggregation of birds, requires measuring the classical costs and benefits of coloniality and their net effect.

## 8. SEXUAL SELECTION AND COLONIALITY

Another hypothesis proposed to explain the evolution of avian coloniality is that colonies reflect clustering by males in response to mating preferences of females. Although recently promoted as a new perspective on coloniality (Wagner *et al.*, 2000; Danchin and Wagner, 1997), the idea behind this hypothesis can be traced back at least to Collias and Collias (1969). They studied the polygynous Village Weaver (*Ploceus cucullatus*), finding that small colonies had a smaller proportion of resident females per male. Collias and Collias (1969) suggested that coloniality resulted from the increased efficiency of attracting mates when males clustered. A similar hypothesis was proposed by Draulans (1988), who suggested that groups of males are more conspicuous to females. If solitary males are less likely to be found by females, grouping could lead, on average, to higher mating success.

More recent refinements are based on the observation that females of many apparently monogamous species engage in extra-pair copulation (see Section 5.2.1), and their seeking of extra-pair matings with high quality males might lead to settlement by other males in high density around the favored males (Wagner *et al.*, 2000; Wagner, 1997, 1993). The process is suggested to be similar to the "hotshot" model of lek evolution (Hoglund and Alatalo, 1995; Beehler and Foster, 1988), and Wagner (1999) suggests that colonies represent "hidden leks" in which males cluster together for purposes of mating. Grouping by males may also be promoted by active female preference for groups, again similar to that proposed for leks (Hoglund and Alatalo, 1995; Bradbury, 1981), in which females prefer to compare-shop among males in a group and are less likely to consider solitary ones. The idea that coloniality might arise from processes of sexual selection is attractive because it focuses on the behavior of individuals early in the breeding season when settlement actually occurs.

bility is that initial aggregation may have been promoted by heterogeneity in resources such as food, with birds initially clustering to take advantage of local environmental conditions (Boulinier and Danchin, 1997). Further aggregation may have been driven by increasing success as a result of the social benefits of coloniality. To date, we have no direct information to test these possibilities in any species.

The problem of what prevents formation of a few supercolonies has also not been satisfactorily explained. Wagner (1999) suggested that breakdown in a site's autocorrelation reflected its quality changing over time, which prevented continued colony growth, and data for Black-legged Kittiwakes and Cliff Swallows seem to show this (Brown *et al.*, 2000; Danchin *et al.*, 1998). Yet, if autocorrelation is high over any one-year period, successive years should represent a nonindependent chain with similar overall site suitability: Year 2, which was similar to year 1, should be similar to year 3, which in turn should be similar to year 4. Perhaps the chain is broken by catastrophic events such as floods or storms, but if this occurs often, information on past performance becomes less useful. As the difference between good and poor sites and the degree of autocorrelation in reproductive success at a site increase (both of which are needed to promote coloniality under this model), good sites should attract most birds, and inevitably all individuals should concentrate in one or a few enormous colonies (Brown and Rannala, 1995). Although colonies are indeed huge in some seabird species and others such as Tricolored Blackbirds, most species show extensive variation in colony size (Brown *et al.*, 1990). Persistence of small colonies is not easily explained by the habitat selection model.

Nevertheless, the incorporation of habitat-selection mechanisms into thinking about coloniality is a major advance. Forbes and Kaiser's (1994) and Danchin and Wagner's (1997) performance-based model may be particularly useful in helping to explain or to predict change in colony sizes from one year to the next. This was illustrated well in our study of Cliff Swallows (Brown *et al.*, 2000). For example, we found that successful sites the previous year are initially reoccupied, probably through strong philopatry of previous residents. Nonbreeders and failed breeders from the prior year then select among the occupied subset of sites based on their assessment of conspecific performance the previous season, and naive first-year birds settle in the larger colonies because they are attracted to conspecifics (Brown and Rannala, 1995; Podolsky and Kress, 1989; Burger, 1988; Stamps, 1988). This promotes colony growth of previously successful sites. In contrast, an unsuccessful site has fewer past residents return because they were unsuccessful the previous year and they therefore disperse. Such a site is also unlikely to

Little if any data are available to determine whether bird colonies result from mating preferences, and the existing data do not provide a conclusive test. The best data still seem to be those of Collias and Collias (1969) on weavers. Males in large colonies had more mates, suggesting that females preferred to settle in larger groups. Collias and Collias ruled out size of nesting trees as a possible influence on colony size and female settlement, although they had no information on male quality among different colonies. It may be easiest to detect female clustering in polygynous species such as weavers, where female settlement is not constrained by pair bonding and social monogamy.

More recently, observations on Razorbills (*Alca torda*) and Purple Martins have been offered to support the hypothesis that coloniality is linked to mating strategies (Wagner, 1999, 1997; Wagner *et al.*, 1996). Colonial Razorbills form mating arenas similar to leks near their colonies where both males and females travel for the apparent purpose of engaging in extra-pair mating (Wagner, 1992). Perhaps coloniality facilitates this behavior just as it may promote social foraging away from nests. However, it is unclear what fitness benefits either male or female Razorbills derive from extra-pair mating, and some advantage is necessary for it to promote coloniality. In Purple Martins, extra-pair copulations occur commonly in colonies, with older males tending to achieve most of the extra-pair fertilizations, primarily with the mates of younger males (Wagner *et al.*, 1996; Morton *et al.*, 1990). One male achieved 87% of all detected extra-pair fertilizations in the colony, and coloniality was suggested to be an outcome of female settlement around such preferred males (Wagner *et al.*, 1996). Morton's and Wagner's work on martins demonstrates clearly how fitness payoffs from coloniality can differ substantially among individuals within the same colony. However, their data do not show that colonies form for mating advantages to either sex, in part because they did not have comparative data on mating success of individuals in colonies of different sizes or nesting solitarily. In Bearded Tits (*Panurus biarmicus*), extra-pair mating advantages to females also were suggested as a selective pressure promoting coloniality, but the study's principal empirical result was only that extra-pair copulations were more frequent in colonies than among solitary nesters (Hoi and Hoi-Leitner, 1997).

Demonstrating that females in colonies seek extra-pair copulations more frequently than solitary females could be simply a consequence of the many potential mating partners in colonies (see Section 5.2.1). To test properly the sexual selection model for coloniality, one needs data on the choices made by females when settling. Do they avoid solitary males or ones in small groups and preferentially recruit to large colonies, and do they solicit matings in these large colonies? It is also

necessary to know what benefits, if any, females derive from extra-pair matings, and how average fertilization success of males differs between colonies and solitaries. No study of birds has addressed all of these questions, but observations of Great Frigatebirds (*Fregata minor*) suggest that females may prefer larger clusters of males within colonies when prospecting for mates early in the year (Reville, 1988). In contrast, female Lesser Frigatebirds (*Fregata ariel*) do not seem to prefer males in larger groups (Reville, 1991). In colonial Longear Sunfish (*Lepomis megalotis*), females do not prefer males that cluster, and solitary males achieve higher success (Jennings and Philipp, 1992). The sunfish results in particular do not support a sexual-selection interpretation of coloniality.

Recent work on Red-winged Blackbirds (*Agelaius phoeniceus*) by Weatherhead (1999) and Humboldt Penguins by Schwartz *et al.* (1999) suggests caution in interpreting extra-pair mating as any sort of finely tuned behavioral strategy. In one of the few studies to follow mating tendencies of females across years, Weatherhead found that paternity patterns of females were inconsistent; females that engaged in extra-pair mating did not prefer the same males each year, and females switching mates between years did not preferentially choose their extra-pair partners as mates. Some females engaged in extra-pair mating one year but not the next. In Humboldt Penguins, females that solicited extra-pair copulations in one year remained with the same male as a mate in the second year (Schwartz *et al.*, 1999). Female Red-winged Blackbirds apparently do not improve the genetic quality of their offspring through extra-pair mating (Weatherhead, 1999). Similarly, extra-pair copulation, while very common, appears to be an inefficient reproductive tactic in colonial Ross's and Snow Geese and Humboldt Penguins, with only 2–5% of young in geese and 0% in penguins resulting from extra-pair mating (Dunn *et al.*, 1999; Schwartz *et al.*, 1999). If these results hold for other birds, the evolutionary impact of extra-pair mating in general and on the evolution of coloniality in particular may be greatly overstated in our current thinking.

Although colonies clearly influence mating strategies of both males and females due to proximity of conspecifics, it appears premature to accept either extra-pair mating or greater conspicuousness of males as primary factors in the formation of bird colonies until better data are gathered. Opportunities for females to comparison-shop among males and potentially to engage in matings with multiple high-quality males more likely are consequences of coloniality in birds that initially clustered for other reasons. Høglund and Alatalo (1995) reached a similar conclusion about the "hotshot" hypothesis and lekking.

A recent phylogenetic study of the relationship between coloniality



and mate retention (Dubois *et al.*, 1998) also suggests that mating strategies do not evolve simultaneously with coloniality but instead are more likely byproducts of breeding aggregations. Highly colonial waterbirds tend to exhibit high rates of divorce between seasons, possibly because colonies provide greater opportunities to assess other potential partners and to change to a higher quality mate the next year (but see Weatherhead, 1999). Waterbirds that occupy small colonies tend to be more faithful to their mate between seasons (Dubois *et al.*, 1998). However, the phylogenetic analysis shows that mate fidelity tends to evolve after (not at the same time as) the transition from high to low degrees of coloniality (see Section 3). Most likely, coloniality and mate retention in the taxa studied may be related to some third variable, such as stability of habitat and degree of nomadism (Dubois *et al.*, 1998). Still, the greater ability to assess potential mates in a large colony (particularly for second nesting attempts within a season) is probably a potentially important benefit of coloniality, even if it did not initially lead to grouping.

## 9. VARIATION IN COLONY SIZE

The fact that some colonial birds have highest mean reproductive success in colonies of particular sizes (Table I) suggests that selection should remove individuals that use the less successful colonies. The paradoxical persistence of colony sizes larger or smaller than the apparently most successful has puzzled ornithologists for decades and remains one of the biggest enigmas associated with coloniality. Most colonially breeding birds show colony-size variation of several orders of magnitude within populations, and this variation is seen in all taxonomic groups (Brown *et al.*, 1990).

As illustrated, for instance, in almost every issue of *Colonial Waterbirds*, there is a huge descriptive literature on site use in colonial birds, especially ciconiiformes, larids, and alcidids, some of which has considered variation in colony size. However, almost all of this work has tended to cast colony-size variation in terms of physical environmental variables (e.g., height of tree, distance to open water, type of vegetation, grass cover on beaches, etc.). These studies have tended to be species-specific in their interpretation and few general principles have been proposed. Others have taken advantage of natural variation in colony size to explore many of the costs and benefits of coloniality (see Section 5), but even these have tended not to consider until recently why colonies vary in size.

Several hypotheses to explain why colonies vary in size have been

proposed (Brown *et al.*, 1990). Among these, the two most likely to have wide applicability are: (1) colony size tends to reflect local resource availability, with birds distributed in habitat patches roughly in ideal-free proportion to local resources such as food or nesting sites (Davis and Brown, 1999); and (2) colony-size variation reflects different phenotypic or genetic characteristics of individuals, with some birds benefiting the most from larger colonies and others benefiting the most from smaller colonies (Brown and Brown, 2000b, 1999b, 1996). On the other hand, the instability of colony size caused by the free movement of individuals into and out of groups might also suggest that birds are not sensitive to differences in colony size and that we are being misled in focusing on it.

### 9.1. Ideal-Free Distributions and Local Resources

That colony size might reflect an ideal-free distribution of birds with respect to patchy resources within a habitat has been essentially the only widely discussed hypothesis for colony-size variation (Danchin and Wagner, 1997; Brown and Brown, 1996; Brown and Rannala, 1995; Brown *et al.*, 1990; Shields *et al.*, 1988). This view holds that local variation in resources or intrinsic habitat quality leads to occupancy by birds in direct relation to resource abundance. Resources may include amount of food or number of nesting sites and potential mates, or aspects of nesting habitat quality such as relative degree of predation or ectoparasitism experienced. The net effect is that more birds settle in areas of high resource abundance and fewer birds in areas with low abundance. If the distribution is truly ideal free (with continuous input of resources), each individual regardless of where it settles receives an equal share of the total resources in the habitat as a whole. Colony-size variation would then reflect variation in intrinsic quality of habitat patches.

The association between patchy resources and coloniality has been recognized for decades (Danchin and Wagner, 1997; Alexander, 1974; Horn, 1968; Crook, 1965, 1964). Furthermore, ideal-free theory has been well studied and the concept applied frequently to foraging groups of different sizes (reviewed in Tregenza, 1995). However, no one has studied directly whether breeding colonies represent ideal-free distributions with respect to resources or correlate in other ways with resource availability. Brown and Rannala (1995) indirectly tested whether Cliff Swallow colonies reflect an ideal-free distribution by comparing observed colony sizes at sites across years to a theoretical distribution based on a Poisson process. Making the assumption that resources at a



site are autocorrelated between years, they found that swallows were not distributed among sites in an ideal-free way. This approach has promise, but it is informative only when empirical results differ from the theoretical distribution (rejecting the ideal-free distribution). If data fit the model, the ideal-free distribution cannot be confirmed because other processes may generate the same distribution of colony sizes. In Purple Martins, colony size is roughly proportional to the number of nesting cavities available, and all birds have equal success regardless of colony size. This led Davis and Brown (1999) to suggest that martin colonies are ideal-free distributions with respect to nesting-site resources.

The best test of the hypothesis that colonies represent ideal-free distributions would be to measure local resources directly. This requires identifying the relevant resource(s) in a habitat patch, which itself is a major challenge because so many potentially affect colony size (Danchin and Wagner, 1997; Brown and Rannala, 1995; Section 4). More total resources should be associated with larger colonies. Perhaps the most obvious resource to influence colony size in this way is food. There is, however, relatively little information available on food abundance at colonies of different sizes (see Section 6.4). An alternative approach of assessing the amount of foraging habitat near colonies of different sizes, assuming that a greater foraging area supports more food, has been used in studies of several species of herons (Gibbs and Kinkel, 1997; Farinha and Leitao, 1996; Gibbs *et al.*, 1987; Fasola and Barbieri, 1978; Werschkul *et al.*, 1977) and in Rooks (*Corvus frugilegus*; Griffin and Thomas, 2000). Amount of preferred foraging habitat within a colony's foraging range correlated directly with colony size in these species. The results, if general, would imply that colony size reflects local resource availability, and also would suggest that colony formation occurs in response to patchy and uneven resource distributions.

In assessing any relationship between colony size and local resources, it is important to distinguish to what degree resource abundance causes colony size and to what degree it reflects the consequences of colony size. If birds initially choose sites based on food availability early in the nesting season, at that time we might expect to see a positive relationship between local food resources and colony size. However, a possible consequence of larger colony sizes is food depletion over time (see Section 6.4), which may eventually reduce local food availability. If resources were measured later in the season, we might find no relationship (or an inverse one) between food availability and colony size.

Another form of the ideal-free distribution incorporates despotic behavior by residents already settled (Ekman, 1989; Fretwell and Lucas,

1970). In this case, some birds actively regulate colony size by aggressively excluding later arrivals from a site, potentially resulting in a greater per-capita fraction of the total resource for the despots. There is some evidence that colony residents at times prevent later arrivals from settling in Yellow-legged Gulls (*Larus cachinnans*; Bosch and Sol, 1998), Black-legged Kittiwakes (Porter, 1990), and Yellow-rumped Cuckoos (Robinson, 1986). Despotic behavior might also cause apparent discrepancies in the ratio between colony size and total resource availability. Clearly, before colony size as an ideal-free distribution can be properly evaluated, one must determine the effects of the costs and benefits of colony size on local resources and whether despotic behavior occurs.

Given these difficulties, it is not surprising that we have little data bearing directly on whether avian colony sizes reflect ideal-free distribution of individuals. However, it seems likely that heterogeneity in resources within a habitat contributes in part to colony-size variation among birds, at least in the colony selection phase and perhaps even in species in which the social costs and benefits of group size have a large separate influence on fitness. We need additional measurements of resource availability around colonies of different sizes. The extensive development of ideal-free theory (Tregenza, 1995) provides a rich framework for studying variation in colony size.

## 9.2. Phenotypic and Genetic Differences among Individuals

Much of the empirical work on avian coloniality has focused on the average expectations of birds in different colonies, commonly analyzing how mean values of a cost or benefit vary with colony size (see Section 7.1). However, breeding colonies are usually made up of individuals of different ages, with different backgrounds and experience, and of varying physiological condition. These birds may receive different net advantages from colonial nesting; for example, the greater overall vigilance possible in a large colony (see Section 5.3.1) may improve the odds that a naive, young bird will survive the breeding season more so than for an older, experienced individual. The within-colony asymmetries in the expected costs and benefits imply that not all birds in a colony receive the same expected payoffs of a given colony size (Brown and Brown, 1996; Morton *et al.*, 1990; Møller, 1987) or that not all individuals formed colonies for the same reason (Blanco and Tella, 1999; Jenni, 1993; Still *et al.*, 1987; Summers *et al.*, 1987; Weatherhead, 1983; Krebs and Barnard, 1980).

Variation in colony size between sites may reflect these different

expectations and abilities of individuals (Figure 1; Brown and Brown, 2000b, 1996). Among foraging animals, competitive ability may affect choice of group size: Low-ranking fish prefer to feed alone rather than in a group because they cannot compete for food in large groups (Ranta *et al.*, 1993). The notion of sorting among groups based on competitive ability has been applied to groups of cooperatively breeding birds (Brown, 1982), fish schools (Ranta *et al.*, 1993; Ranta and Lindstrom, 1990), and bird leks (Hoglund *et al.*, 1993). Ideal-free theory that takes into account unequal abilities of individuals (reviewed in Tregenza, 1995) makes essentially the same prediction that phenotypic or genetic characteristics of birds will influence their expectation of success in different habitats. We suggest that application of unequal-competitor ideal-free models to avian coloniality would be instructive (see Jones, 1987). Variation in colony size provides a natural basis on which to examine differences in individual performance.

The first step in testing the hypothesis that individuals' attributes differ among colonies is to ask to what degree colonies differ in their composition. For example, are young, inexperienced, or otherwise inferior individuals relegated to small colonies (as in fish schools), while high-quality birds settle in larger colonies? If so, this implies that sites differ in their intrinsic quality and that large colonies probably form in the best areas. Such a pattern also means that observed differences in reproductive success cannot be attributed solely to site quality or local resources; nesting success may also reflect in part the social benefits (predator avoidance, food-finding) that accrue whenever large numbers of high-quality birds aggregate.

To date few field studies have examined differences in composition among colony sizes. In Gentoo Penguins (*Pygoscelis papua*), Northern Fulmars (*Fulmarus glacialis*), Black-legged Kittiwakes, Black Skimmers (*Rynchops niger*), and other seabirds, younger birds are suspected to settle in small colonies (Burger and Gochfeld, 1990; Kharitonov and Siegel-Causey, 1988; Robertson, 1986; Coulson and White, 1958, 1956; Fisher and Waterston, 1941). Small colonies consist of birds of low body mass and apparent poor quality in Yellow-rumped Caciques (Robinson, 1986, 1985). In Bearded Tits, females living in colonies tended to weigh more and were thus in better condition than birds nesting as solitary (Hoi and Hoi-Leitner, 1997). If these differences in condition applied to the birds at the time they settled and were not mostly consequences of the birds' having lived in colonies of different sizes prior to being measured, Hoi and Hoi-Leitner's results imply that better quality females aggregate. In Eurasian Tree Sparrows, individuals moved between colonial and solitary nesting whenever their nesting success was low,

suggesting that individuals are sensitive to differences in social environment and that colonial versus solitary nesting is a conditional strategy (Sasvari and Hegyi, 1994). In Bank Swallows, older individuals secured the best nesting sites within colonies, forcing formation of smaller sub-colonies composed of younger birds (Jones, 1987). Sorting may be passive in which low-quality birds simply avoid the areas of high population density, or it may be mediated by aggressive interactions in which the low-quality birds fail to secure breeding sites when they lose contests in favored areas.

A different situation seems to apply in Cliff Swallows. Cross-fostering experiments indicate that choice of colony size has a strong heritable basis (Brown and Brown, 2000b). When newly hatched nestlings were transferred between large and small colonies and their breeding-colony choices as yearlings monitored, individuals chose to settle in colonies that matched the size of their birth colony but not that of their rearing colony. In this case, variation in colony size within the population probably is caused by a polymorphism in genetic preferences linked to how different individuals perform in groups of different sizes (Brown and Brown, 2000b). This is the only study to date to examine whether variation in colony size might be based on genetic differences among birds in groups of different sizes. However, choice of colony size in Cliff Swallows is not entirely genetically based, as some individuals tend to begin their breeding careers in large colonies and switch to smaller colonies as they get older (Brown and Brown, 1996). Possibly naive first-year swallows gain more from the antipredator and foraging advantages of a large colony (despite the costs) than do more experienced birds. Older individuals may switch to smaller colonies to avoid the substantial costs of larger colonies (ectoparasitism in particular), which apply to all birds regardless of their age. This suggests that experienced birds who have less to gain from the advantages of a large colony prefer smaller colonies to minimize the costs of group life. A similar trend for older females to prefer solitary nesting was suggested for Eurasian Tree Sparrows (Sasvari and Hegyi, 1994).

Determining the composition of colonies and the attributes of colony members should be a priority in future field studies. Interpreting patterns of reproductive success (Boulinier and Danchin, 1997; Danchin and Wagner, 1997) will be influenced by colony composition: How much of the success at a site is determined by intrinsic habitat features and how much by the phenotypic or genetic characteristics of colony residents? If the latter is a major component of the observed reproductive success, prospective residents are unlikely to learn much about future prospects at a site by observing nesting activity (*sensu* Danchin

and Wagner, 1997), unless colony composition between years stays the same.

### 9.3. (In)stability of Colony Size

We have suggested that colony size reflects an adaptive strategy by individuals who sort among colonies until they find the one yielding maximum fitness, based on their own needs (see Brown and Brown, 1996). That colony size itself can be selected for was shown in studies of Fieldfares, in which geographic differences in average colony size reflect the relative risk of different types of predation and chick starvation in different regions of Sweden (Wiklund and Andersson, 1994). However, colony size is potentially unstable (Pulliam and Caraco, 1984; Sibly, 1983). An individual may freely join or leave a colony, thereby changing its size; these size changes are beyond the control of residents already settled. If there is an optimal colony size that in theory provides the highest fitness for members, individuals who seek to join the colony from the outside will alter the payoffs for all residents by increasing the colony size above the optimum. As a result, groups larger than the optimum might be common (Zemel and Lubin, 1995; Pulliam and Caraco, 1984). Theoreticians have modeled the conditions under which individuals should and should not join groups of particular sizes (Rannala and Brown, 1994; Giraldeau and Caraco, 1993; Higashi and Yamamura, 1993; Giraldeau and Gillis, 1985; Sibly, 1983). The presumed instability of colony size has led to questions about whether it provides an appropriate framework for analyzing fitness of colonial animals (Wagner *et al.*, 2000; Møller, 1997) and thus whether animals can use it as a reliable cue in selecting where to nest (Brown and Brown, 1996; Kharitonov and Siegel-Causey, 1988). Others have implied that site characteristics per se are more likely than colony size to determine fitness (Danchin and Wagner, 1997).

However, stability of group size depends heavily on the shape of the fitness function associated with group size. If fitness declines steeply in groups larger than the optimal, an individual seeking to join an existing group at optimal size may do better by remaining as a solitary or joining a smaller group (Giraldeau and Gillis, 1985). This may occur especially in cases where competition is increased in large groups. Stability of group size will also depend on relatedness between the potential joiner and members in the group: If relatedness is high, a potential joiner may be selected to avoid the group because its presence would depress fitness of all its relatives within the group (Giraldeau and Caraco, 1993; Higashi and Yamamura, 1993). This probably applies more

often to social insects than colonial birds but may be important for cooperatively breeding birds that live in family groups of various sizes (Brown, 1982). Thus, before we can know whether an optimal colony size is stable or unstable, information on both fitness (reproductive success) and relatedness in relation to colony size must be obtained. Despotic behavior (see Section 9.1) may also regulate colony size and potentially keep it near an optimum.

The assumption that optimal group sizes exist at all may be problematic, because there is little evidence for optimal breeding colony sizes in general (see Section 7.1; Table I). If colonies form in an ideal-free way with respect to habitat quality, one would predict no optimal colony size. The lack of a relationship between reproductive success and colony size in 25 studies is consistent with there being no optimal colony size, and only three of the total 64 studies provided even weak evidence for an intermediate optimal colony size (Table I).

Finally, colony sizes can be stable if individuals coordinate their selection of colony. If individuals seeking to join colonies aggregate prior to settlement (e.g., during migration or foraging), they can colonize entirely new sites and come much closer to achieving a desired colony size than if they each joined an existing group separately. In various seabirds and Cliff Swallows, birds move in and out of colonies early in the season in groups (Brown and Brown, 1996; Kharitonov and Siegel-Causey, 1988), suggesting some collective decision-making. Many sites are first occupied by groups, and birds arrive on the breeding grounds in flocks. The assumption that birds looking for colonies operate independently needs to be tested, because this may not be true in general. Colonial birds, well known for their aggregative tendencies, might show greater parallels with the collective decision-making of the social insects (Seeley, 1995) than generally appreciated. Clearly more must be learned about the mechanisms of colony choice before we can know whether the behavior of individuals seeking to join groups from the outside represents a potential constraint on achieving a given colony size at a site.

The huge body of literature on how the costs and benefits of coloniality vary with colony size (see Section 5) shows that the number of conspecifics breeding at a site can have a major effect on fitness, regardless of local environmental conditions or habitat quality. With these effects so substantial, it seems unlikely that the animals themselves would not have been selected to be sensitive to the consequences of settling in groups of different sizes. The recent work showing heritability of colony-size choices in Cliff Swallows (Brown and Brown, 2000b) supports this conclusion.

## 10. PROSPECTUS

Coloniality remains the least understood of avian social systems. Fundamental gaps remain in our understanding of the causes of breeding aggregations, and as we have tried to illustrate in this review, much of the conventional wisdom about avian coloniality is based on shaky and equivocal data. This form of social behavior is enormously complex, and analyses of single factors are unlikely to be useful. Researchers have sought a general explanation for coloniality that applies across species, perhaps because of the success of kin selection in explaining cooperative breeding (Brown, 1987; Wilson, 1975; Hamilton, 1964), but increasing evidence shows that there may be no single evolutionary origin of coloniality. The behavior appears labile and apparently arises in response to various ecological factors, most of which are still unclear in most species.

The three commonly cited selective pressures thought to promote coloniality—predator avoidance, better food-finding, and nesting site shortage—appear to apply in different species, but the overall importance of each in the evolution of coloniality is unknown. There has been extensive debate about which of these are likely to be important in general; the debate has generated many strongly held opinions but ones based on little field data. Critical analysis of the data available suggests that antipredator advantages and aggregation in response to limited nesting sites may not be as pervasive selective pressures as many have claimed. Field studies (Brown and Brown, 1996), theoretical analyses (Buckley, 1997; Richner and Heeb, 1996, 1995), and phylogenetic comparisons (Beauchamp, 1999a; Rolland *et al.*, 1998) now suggest that coloniality may most often be associated with patchy food resources and social foraging, although proper comparative studies of feeding efficiency in colonial birds are still few in number.

Our work on Cliff Swallow coloniality has revealed many effects on fitness that can be attributed to group size (Brown and Brown, 1996), and we suspect that a similar effort on other species would produce comparable results. These costs and benefits are themselves interesting, but individually they tell us little about the evolution of coloniality. We agree fully with Danchin and Wagner's (1997) call for greater emphasis on measuring reproductive success in colonial species, because reproductive success integrates all costs and benefits into a single, evolutionarily relevant measure of fitness. The first step in any study of coloniality should be to document how reproductive success varies with colony size, because that may suggest whether colonies provide active advantages from conspecific association or whether they result largely

from limited nesting sites or reflect ideal-free aggregations at resources. Then, how those patterns of reproductive success are generated can be addressed by focusing on the individual costs and benefits of coloniality. Also, with the resurgence of interest in "Allee effects" and their implication for conservation and population biology (Courchamp *et al.*, 1999; Stephens and Sutherland, 1999), documenting how reproductive success varies with group size should be of wide interest. Colonial birds present splendid opportunities to measure the reproductive consequences of undercrowding or overcrowding and how these may affect population ecology.

Many of the past studies of reproductive success in colonial birds have inherent limitations, often related to the small number of colonies studied or to the pooling of data (Table I), and thus a clear need exists for additional studies specifically designed to measure reproductive success in a wide range of colony sizes. Countless studies of colonial birds have been conducted at a single colony site only. These have yielded little insight into the evolution of coloniality because they do not include rigorous simultaneous comparisons of birds in clearly different social settings with yearly variation controlled. We also urge that researchers, including ourselves, adopt greater statistical rigor in the design and analysis of field data collection on colonial birds. For example, in our review of work on reproductive success (Table I), we found many instances where nests from the same colony were treated as independent data points when they should have been combined into a single per-colony measure and each colony or colony size treated as the sampling unit (Brown and Brown, 1996). Another challenge facing workers on coloniality is how to sample colonies. Large colonies in particular usually require selection of a sample of nests for study. Because of spatial and temporal differences among individuals within colonies, samples to be unbiased need to be chosen randomly, with each nest regardless of its position or timing having an equal probability of being selected. Few field studies on colonial birds have explicitly adopted random sampling, and thus virtually all published data may be biased in unknown ways related to nest accessibility, spatial position, or timing. Cluster sampling techniques (Cochran, 1977) would be of value for field work on coloniality; these methods and random sampling have been used rarely to our knowledge (see Rannala, 1995; Scolaro, 1990).

The most glaring deficiency in current theory on coloniality is in understanding what causes variation in colony size. Most animals that form groups of any kind at any time of the year show extensive variation in group size within and between populations. Ecologists have recognized that different group sizes have profound effects on many aspects

of life history and behavior, including foraging (Caraco *et al.*, 1995; Janson, 1988; Clark and Mangel, 1986, 1984; Caraco, 1981), mating tactics and sperm competition (Andersson, 1994; Birkhead and Møller, 1992), cooperative breeding (Hoogland, 1995; Brown, 1987, 1982), habitat selection (Podolsky and Kress, 1989; Stamps, 1988; Burger, 1981; Fretwell and Lucas, 1970), spread of parasites and disease (Brown and Brown, 1986; May, 1983; Hoogland and Sherman, 1976; Black, 1966), and communication (Waser and Wiley, 1980; Smith, 1977). Yet the consequences of varying group sizes are much better known than the causes. Coloniality provides a natural framework in which to analyze the fitness consequences of different group (colony) sizes, and the link between group size and fitness is more direct and, by measuring nesting success, easier to establish in colonially nesting birds than in, for example, foraging groups.

We urge that investigators begin analyzing the phenotypic and genetic differences between individuals in colonies of different sizes. The limited information available suggests that there can be profound differences in individuals' attributes between colonies, and these differences confound interpretations of most of the classical costs and benefits of coloniality. Different individuals are likely to receive different payoffs from colonies of different sizes, potentially accounting for variation in group size within a population (Figure 1). We also need studies designed to manipulate experimentally colony sizes or resource availability. By measuring performance of the same individuals both before and after the manipulation, we can test whether certain individuals are indeed adapted to groups of different sizes or whether colony size reflects some sort of matching between population density and resource abundance. We encourage study of proximate habitat-selection mechanisms (Bouligner and Danchin, 1997; Danchin and Wagner, 1997), because these may yield insight into why colonies change in size between years, a question with both theoretical and practical (management) implications.

Most of the empirical and theoretical work on avian coloniality has centered on behavioral or ecological issues. Little consideration to date has been given to the effect of coloniality on genetic structure of populations. A colony represents a breeding population, which, depending on the degree of immigration between sites, may or may not be relatively closed. If immigration and thus gene flow is infrequent, levels of inbreeding or genetic differentiation may be high (Chepko-Sade and Shields, 1987; Rockwell and Barrowclough, 1987). Studies using molecular markers show that some colonial seabirds exhibit genetic differentiation between or even within colonies (Friesen, 1997). The spatial distribution of colonies allows us to test whether population structuring

comes about through "island," "stepping-stone," or other models of gene flow (*sensu* Wright, 1969). Although few studies have taken advantage of colonial birds to test population-genetic theory, Rannala (1995) used populations of swallow bugs (*Oeciacus vicarius*) inhabiting Cliff Swallow colonies to examine how demography affects genetic structure.

Incorporation of population genetics into our ecological and behavioral thinking about coloniality may offer unexpected insights; for example, egg hatchability, thought generally to be an index of genetic similarity among parents, is lower in smaller colonies of Cliff Swallows, suggesting that decreased odds of mating with a relative might be an other advantage of occupying a large colony (Brown and Brown, 2001). Other studies have shown morphological differences among birds inhabiting different colonies (Brown and Brown, 1996; Rasmussen, 1994; Moen, 1991; Schreiber and Schreiber, 1988; Birkhead, 1984; Birkhead and Nettleship, 1981), consistent both with genetic differentiation within a population and the sorting of phenotypes among groups. One of the new frontiers in the study of coloniality for the 21st century will be how genetic structure of populations and source-sink dynamics are potentially affected by nonrandom clustering of individuals in space. This will be facilitated by the relative ease with which demographic and genetic data can be collected from many colonial species.

The future is exciting for researchers interested in avian coloniality. With new hypotheses available to guide us and as we move beyond looking for a single explanation for all bird colonies, the possibilities for exciting discoveries abound. New investigators should not be deterred, because coloniality is clearly an aspect of avian biology where everything is not already known. In many respects we are just starting.

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## CHAPTER 2

## BEGGING IN NESTLING BIRDS

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## 1. PARENT-OFFSPRING CONFLICT

Interest in nestling begging arises from the theoretical conflict over resource allocation between parents and their offspring. This conflict was first proposed by Trivers (1974), who suggested that an individual offspring is selected to obtain a greater proportion of resources than the parent is selected to give. That is, a parent is equally related to each offspring in each brood by half, whereas a nestling is more highly related to itself (i.e., 1.00) than to its present or future siblings (i.e., 0.50-0.25, on average). Conflict between parent and offspring can be expressed throughout the period of parental care from conception through independence, during which offspring are selected to elicit parental investment for a period exceeding the optimum for the parent. Trivers (1974) suggested an offspring is able to "compete" effectively with its parent through psychological manipulation. By begging until its needs have been met, the offspring indicates its degree of distress (for example, its requirement for food) and thereby encourages a higher level of parental investment. In such a system, any offspring signaling a "dishonest" (excessive) level of need would benefit from receiving a level of parental

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