

DOES INTERCOLONY COMPETITION FOR FOOD AFFECT COLONY CHOICE IN CLIFF SWALLOWS?

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Abstract. Explaining why breeding colonies vary in size has been a persistent problem in the study of animal spatial distribution. One hypothesis is that colony size reflects local food availability, which may be affected by the number of conspecifics feeding in a given area. We investigated whether colony size in Cliff Swallows (*Petrochelidon pyrrhonota*) was influenced by competition for food from birds in nearby colonies. Because we knew where Cliff Swallows foraged in relation to their colonies, we could designate for each colony site which neighboring colonies shared its foraging range. If intercolony competition for food is important in the birds' settlement decisions, a negative correlation between a site's colony size and the total number of nests in neighboring sites should result. Among-site analyses within years revealed negative correlations in 8 of 10 years; however, none of the correlation coefficients was significant. Separate among-year analyses for 32 sites revealed none with statistically significant correlations, and the direction of these correlations was not consistent. Annual variability in colony size tended to increase slightly as more colony sites shared the foraging range. Intercolony competition for food in Cliff Swallows does not appear to be strong, perhaps because food is normally abundant and not appreciably depleted by foragers. Also, because of synchronous between-site colony establishment, it may be difficult to predict the number of birds at neighboring sites and thus the degree of future competition at the time individuals settle. Intercolony competition for food may be important only for certain sites or for colonies established later in the year.

Key words: *Cliff Swallow, coloniality, food competition, foraging, habitat selection, Petrochelidon pyrrhonota, social behavior.*

¿Afecta la Competencia entre Colonias por Alimento la Selección de Colonia en *Petrochelidon pyrrhonota*?

Resumen. Explicar por qué existe variación en el tamaño entre colonias reproductivas ha sido un problema recurrente en el estudio de la distribución espacial de los animales. Una hipótesis propone que el tamaño de la colonia refleja la disponibilidad local de alimento, la cual a su vez puede verse afectada por el número de individuos coespecíficos que se alimentan en un área dada. Nosotros investigamos si el tamaño de la colonia en golondrinas *Petrochelidon pyrrhonota* está influenciado por competencia por alimento con aves de colonias cercanas. Establecimos cuáles colonias vecinas compartían áreas de forrajeo basándonos en información sobre dónde forrajeaban las golondrinas en relación a la ubicación de sus colonias. Si la competencia por alimento entre colonias es importante para las golondrinas al decidir dónde establecerse, se esperaría una correlación negativa entre el tamaño de una colonia y el número total de nidos en sitios vecinos. Análisis entre sitios para un mismo año mostraron correlaciones negativas en 8 de 10 años, pero ninguno de estos coeficientes de correlación fue significativo. Análisis inter-anales para 32 sitios por separado no revelaron ninguna correlación estadísticamente significativa, y la dirección de estas correlaciones no fue consistente. La variación anual en el tamaño de las colonias tendió a aumentar ligeramente a medida que más colonias compartían el área de forrajeo. La competencia por alimento entre colonias no parece ser fuerte en *P. pyrrhonota*, posiblemente porque la abundancia del alimento es normalmente alta y no es reducida considerablemente por el forrajeo de las golondrinas. Además, debido a que las golondrinas se establecen de modo sincrónico, sería difícil predecir en ese momento el número de aves presentes en sitios vecinos y por lo tanto, el grado futuro de competencia. La competencia por alimento entre colonias podría ser importante sólo en algunos sitios o en colonias que se establecen más tarde en el año.

INTRODUCTION

One of the most puzzling problems in the study of animal spatial distribution is explaining why breeding colony size varies. In many colonial birds, for example, the smallest and largest colonies within a population vary in size by an order of magnitude or more (Brown et al. 1990). Although we now understand relatively well the costs and benefits of different colony sizes for individuals (e.g., increased parasitism and competition, more efficient food-finding, better avoidance of predators; Brown and Brown 2001), most theoretical and empirical studies of coloniality have not addressed the proximate causes of colony-size variation. Existing hypotheses attribute size variation either to environmental heterogeneity of various types (Horn 1968, Gibbs et al. 1987, Shields et al. 1988, Cairns 1989, Gibbs 1991, Brown and Rannala 1995, Danchin and Wagner 1997) or as a result of phenotypic variation that predisposes individuals toward large or small colonies (Jones 1987, Brown and Brown 1996, 2000, 2001). At present there are not enough field data to evaluate the general applicability of any of these hypotheses.

One of the possible environmental determinants of colony size is local food availability. That animals should distribute themselves in space roughly in proportion to food intake rates is often assumed (and has sometimes been verified empirically; Tregenza 1995). Consequently, we might expect colony size at a given site to reflect the abundance of food in that area. However, the nature of the expected relationship between food availability and colony size is not so clear. Classical ideal-free theory (Fretwell and Lucas 1970) would predict initial formation of larger colonies in areas with more food, yet it has also been argued that larger colonies deplete food over time and lead to intensified competition and lowered food intake rates among colony members (Ashmole 1963, Wittenberger and Hunt 1985, Cairns 1989, 1992, Lewis et al. 2001). Whether colony size is positively or negatively related to local food availability is unknown in most cases, in part because no one has convincingly measured food resources directly at colonies of different sizes in birds or mammals. This is due largely to the many kinds of food most colonial vertebrates consume (requiring many different sampling methods) and the large distances over which they often forage

(Hunt and Schneider 1987, Brown and Brown 1996, 2001).

A few studies, however, have inferred local food availability in relation to colony size by measuring the amount of preferred feeding habitat near a colony (Gibbs et al. 1987, Farinha and Leitao 1996, Gibbs and Kinkel 1997). These studies have suggested that the amount of foraging habitat increases with colony size and that food availability may influence the size of a colony that forms at a site, at least in some herons. Another indirect measure of net food availability (and the focus of this paper) is the extent of use of a colony's foraging habitat by neighboring colonies (Furness and Birkhead 1984). This reasonably assumes that food resources are not infinite, and that as use of a given foraging area increases, competition for food will intensify and food availability will decline. If individuals are sensitive to food availability when making settlement decisions, the size of a colony at any given site should be inversely related to the extent of local competition it experiences from individuals in neighboring colonies. This scenario predicts a negative correlation between colony size at a site and the combined sizes of the neighboring colonies with which it shares a foraging range. Furthermore, by incorporating the potential role of neighbors, we may more easily understand changes of colony size at a given site between years. These size changes are often uninterpretable when a single colony site is considered in isolation.

The value of focusing on potential intercolony competition was illustrated by Furness and Birkhead (1984). For four species of seabirds, they found a strong negative relationship between colony size at a given site and the combined sizes of the other colonies that shared the site's apparent foraging range. This led to the conclusion that these seabirds depleted food resources whenever large numbers of birds fed in a common area, and this reduced food availability led to smaller colony sizes in some areas. Furness and Birkhead's (1984) analysis suggested that net food availability around a site influenced settlement decisions and provided an explanation for why colony sizes in these species varied in size.

Surprisingly, Furness and Birkhead's (1984) approach has rarely been adopted for other colonial species. In one of the few other tests, in Antarctic penguins, Ainley et al. (1995) found

no significant negative correlations between colony size and the sizes of neighboring colonies that shared the foraging range, and for one species they found a significant positive correlation between colony size and the sizes of neighboring colonies. In Rooks (*Corvus frugilegus*), colony size was negatively correlated with the number of potential competitors at six different distances (1–6 km) from a site but was significant only for a 2-km radius (Griffin and Thomas 2000). Whether there was appreciable overlap among colony foraging ranges at 2-km distances was unknown. The Rook study illustrates the difficulty in applying this approach if the foraging ranges of colonies are not known, and this constraint has perhaps discouraged many studies of colonial birds from measuring intercolony competition for food.

In this study we investigate for the first time the role of intercolony competition and foraging range overlap in colony choice by Cliff Swallows (*Petrochelidon pyrrhonota*). We specifically test whether colony size at a site is negatively correlated with the combined sizes of neighboring colonies that share the site's foraging range. The advantage of using this approach with Cliff Swallows is that we know the birds' foraging ranges with certainty and do not have to model the effects of colonies at different distances. We use our results to evaluate whether the extensive variation in colony size seen in Cliff Swallows can be explained in part by differences in net food availability among sites as a result of competition from neighboring colonies. We rely on long-term data on colony size and site usage, spanning 17 years for some sites, and we use information from approximately 100 different colony sites in our Nebraska study area.

METHODS

STUDY ANIMAL AND STUDY SITE

Cliff Swallows are colonial passerines that breed throughout most of western North America (Brown and Brown 1995). They build gourd-shaped mud nests and attach them to the vertical faces of cliff walls, rock outcroppings, or artificial sites such as the eaves of buildings or bridges. Nests tend to be stacked closely, often sharing walls. Cliff Swallows are migratory, wintering in southern South America. At our study site, they arrive beginning in late April or early May, and most depart by late July.

Cliff Swallows feed exclusively on flying insects. They are generalist feeders, with dozens of insect families identified in diet samples (Brown and Brown 1996). Foraging generally occurs in groups and, except in cold weather, at altitudes of 50 m or more. The birds cue on insect swarms transported aloft by localized convection currents, and as a result their food sources are spatiotemporally variable both within and between days (Brown and Brown 1996). Colonies serve as information centers, with birds observing others and following successful individuals to food sources (Brown 1986, Brown and Brown 1996). Past work has shown that virtually all foraging by colony residents occurs within a 1-km radius of a colony site (except in bad weather, when foraging ranges increase), regardless of colony size or habitat type (Brown et al. 1992, Brown and Brown 1996).

Our study site is centered near Ogallala at the Cedar Point Biological Station (41°13'N, 101°39'W), in Keith County, along the North and South Platte Rivers, and also includes portions of Deuel, Garden, and Lincoln counties, southwestern Nebraska. We have studied Cliff Swallows there since 1982. There are approximately 160 Cliff Swallow colony sites in our 150 × 50 km study area, with about a third of these not used in a given year. We included about 100 sites in the analyses for this paper. We excluded colony sites that we did not systematically monitor each season and that therefore had yearly gaps in their histories of usage or size. Those excluded were from the periphery of our study area, and their exclusion should not have affected our conclusions based on sites situated in the core of the study area. Colony size within the Nebraska population varies widely, ranging from 1 to 3700 nests per site. Over a 19-year period, mean (\pm SE) colony size ($n = 1282$) was 356 (± 16) nests. Groups of nests were defined as colonies if the nest owners at least occasionally interacted in foraging or in the mobbing of predators (Brown and Brown 1996); in practice, all the nests on a single bridge or culvert typically constituted a single colony. The study site is described in detail by Brown and Brown (1996).

MEASURING COLONY SIZES

Colony size was defined as the number of nests at a site containing ≥ 1 egg. We determined colony size by doing regular nest checks using a

dental mirror and flashlight inserted through each nest's mud neck, or by estimating the number of active nests by the number of birds regularly present. These estimation methods are presented fully in Brown and Brown (1996). Colony size was recorded for each site each year of the study, giving us colony-size and site-use data for up to 19 years at some sites. However, we excluded the first two years of the study because of uncertainty as to colony-size estimates at some of the sites in those years. Fewer years of data were available for sites first colonized in the later years of the study.

DESIGNATING FORAGING RANGES

Because previous observations had indicated that Cliff Swallows confine their foraging to within a 1-km radius of their colony site (Brown et al. 1992, Brown and Brown 1996), we designated the foraging range for each colony as a 785-ha circle of diameter 2 km centered at the colony site. The only occasions when the birds did not use this colony-centered foraging range was during cold or windy weather when individuals from many colonies would concentrate in hundreds or thousands over lakes or streams and forage on insects just above the water surface, or in canyons where the walls served as windbreaks to concentrate insects. On these occasions birds would travel 3 km or more from their colony sites and mix with birds from many colonies. Bad weather was infrequent enough during most years that we disregarded it in designating foraging ranges. Using topographic maps, we measured the linear distances between all colony sites. We defined any colony within 2 km of a given colony site as a *neighboring colony* with an overlapping foraging range. We scored sites only as overlapping or not, and did not quantify the degree of overlap. However, for a subset of colonies, we investigated whether the degree of overlap had any apparent effect; we did this by comparing colonies that had overlapping neighbors situated at different linear distances within 2 km.

STATISTICAL ANALYSIS

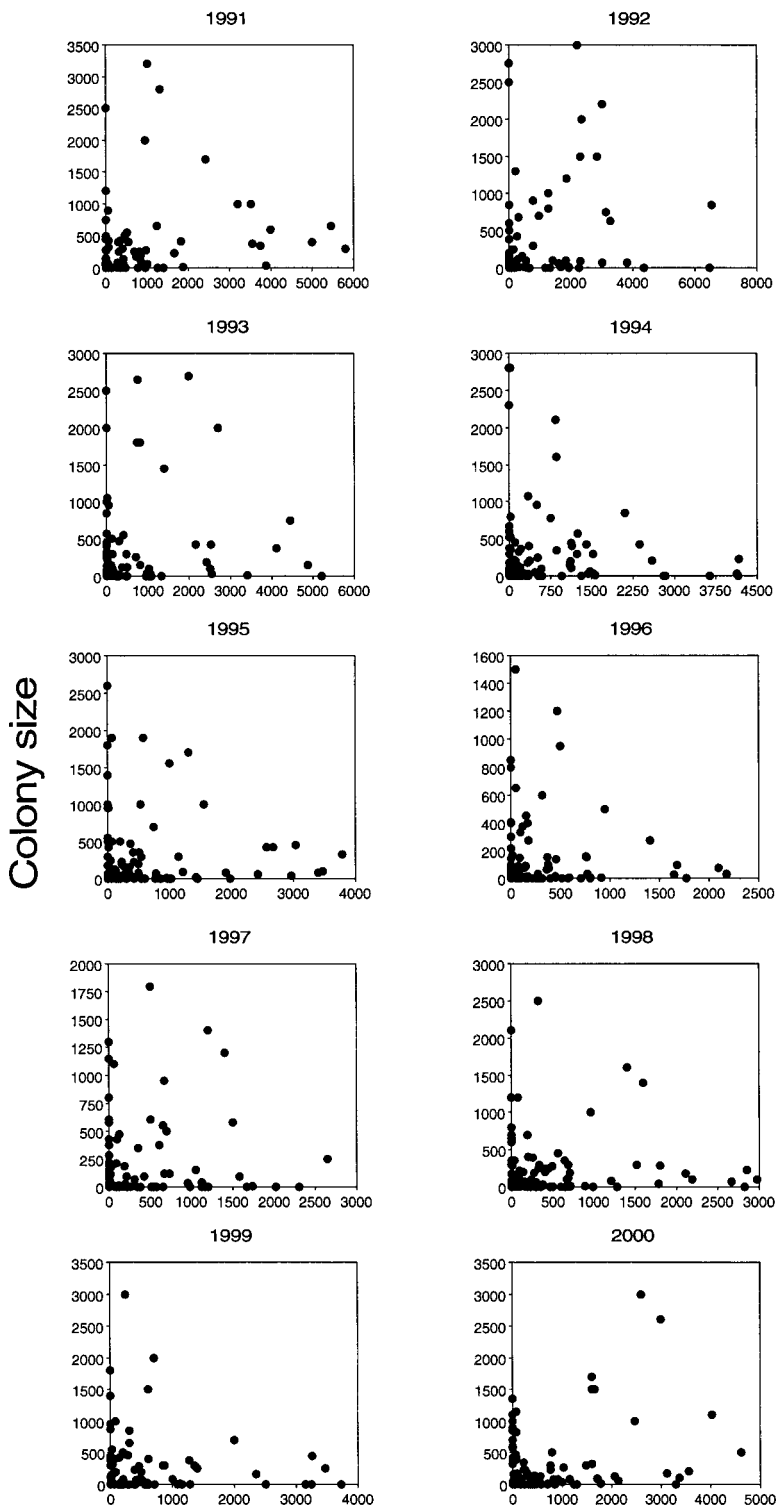
We examined the relationship between colony size at a site and the combined sizes of its neighboring colonies using (1) among-site analyses within a year and (2) among-year analyses within a site. For among-site analyses, we used the 10 years from 1991–2000. For each of these years we used all colony sites for which we had size and neighboring-colony data; this varied from 90 sites in 1991 to 110 in 2000, with the increase reflecting primarily the birds' colonization of new sites during the study. For among-year analyses, we used 41 sites for which we had 15–17 years of data; we arbitrarily established $n = 15$ years as a minimum sample size to ensure some degree of statistical rigor. Paired sites that had only each other as a neighbor counted only once in the calculation of correlation coefficients. In analyses that involved multiple statistical tests, we used the sequential Bonferroni correction (Rice 1989) with an experimentwise error rate of $\alpha = 0.05$ applied to P -values to determine statistical significance. Statistical tests were done with SAS (SAS Institute 1990) and SYSTAT (Wilkinson 1989).

RESULTS

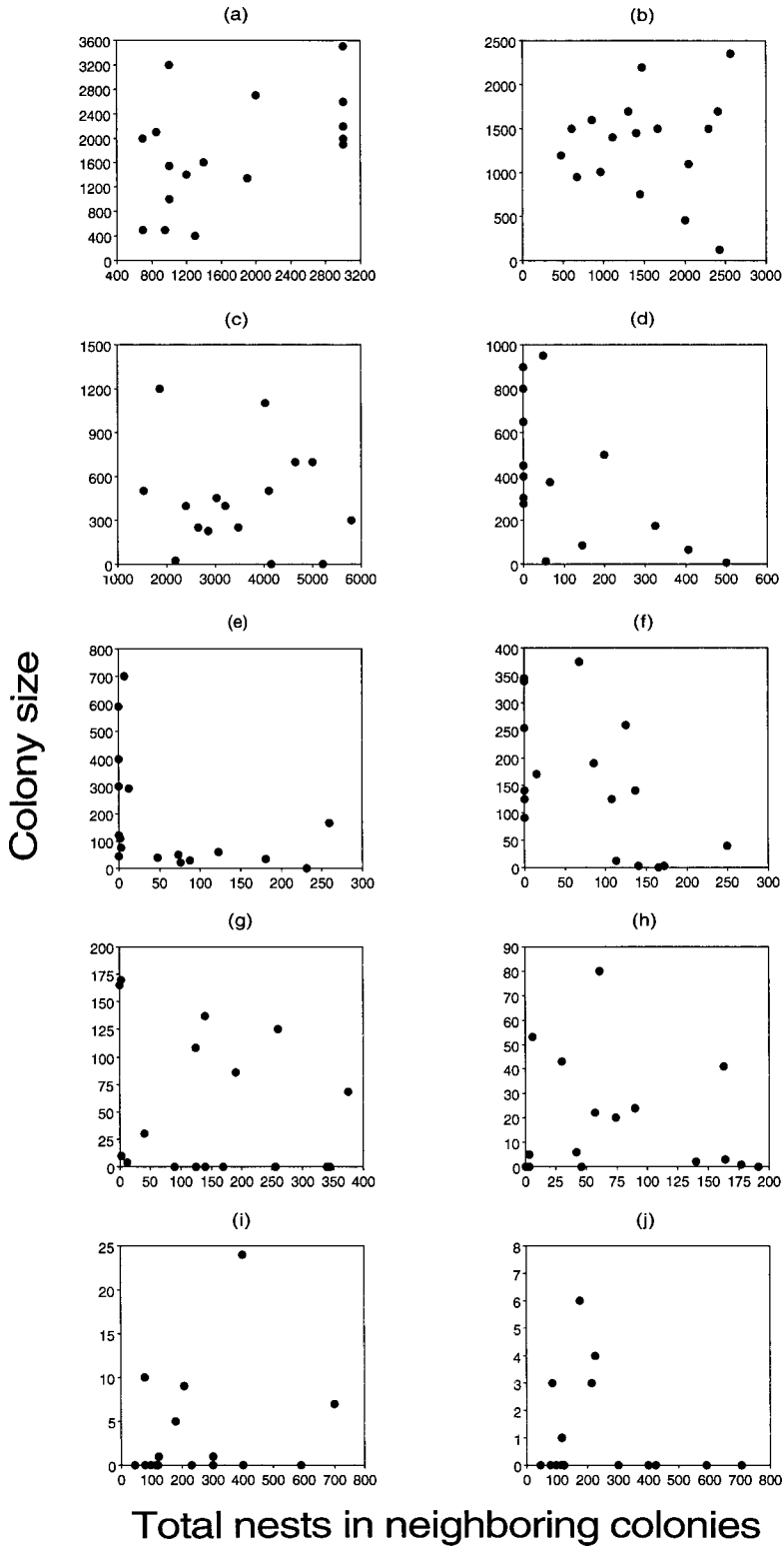
COLONY-SIZE CORRELATIONS AMONG SITES WITHIN YEARS

Rank-order correlations between colony size at a site and the combined colony sizes of neighboring colonies were negative in 8 of the 10 years from 1991–2000 (Fig. 1; r_s ranged from -0.24 to $+0.15$; P ranged from 0.02 – 0.63). Although the general pattern seemed to be for the larger colonies to share their foraging ranges with relatively small colonies, statistically the trends were weak, and none of the correlation coefficients was significant after sequential Bonferroni corrections. The weak statistical relationships may have been brought about partly by the relatively high number of small to moderate-sized colonies (<500 nests) which shared foraging ranges with other small to moderate sized colonies (Fig. 1).

FIGURE 1. Size (number of nests) of Cliff Swallow colony sites in relation to the total number of nests in neighboring colonies (within 2 km) within each year from 1991–2000. →



Total nests in neighboring colonies



COLONY-SIZE CORRELATIONS AMONG YEARS WITHIN SITES

For 32 colony sites with one or more neighboring colonies, we analyzed the change in colony size at a given site among years in relation to the change in colony size of neighboring colonies. These sites varied from a mean annual size of 1.0 to 1794.1 nests. The 32 sites yielded 31 rank-order correlations (two sites had only each other as neighbors and thus allowed only one correlation). Of these 31 correlation coefficients, 13 were negative and 18 were positive ($P = 0.24$, binomial test). None of the correlation coefficients was significant after sequential Bonferroni corrections; Figure 2 depicts relationships for 10 representative sites spanning the size range from small to large (r_s ranged from -0.64 to $+0.50$; P ranged from 0.008 – 0.69). Interestingly, the sites with positive correlations included the pair of colonies (Fig. 2a) in which each was each other's only overlapping neighbor. Both of these colonies were also among the perennially largest colonies in the study area, and thus we might have expected a negative relationship with them in particular if intercolony competition for food influenced settlement decisions. Some sites (e.g., Fig. 2d–f) showed a clear trend for larger colonies to occur in years when few birds from neighboring colonies overlapped their foraging range, but among the other sites there was no obvious among-year relationship between colony size and the number of birds in nearby colonies. Furthermore, there was no apparent pattern in relation to colony size among the sites we investigated: sites that tended to support small colonies annually showed colony-size correlations broadly similar to sites that usually supported large colonies (Fig. 2).

COLONY-SIZE VARIATION IN RELATION TO THE NUMBER OF NEIGHBORING COLONIES

If intercolony competition influences settlement decisions, we might expect colony sites without any competition from neighbors to be more predictable in their size each year than those with one or more neighboring colonies. Among the sites with 15–17 years of size and usage data,

we had nine that had no neighboring colonies overlapping their foraging range. Comparison of the colony-size variation at eight of these neighborless sites (Fig. 3) with those that had neighbors (Fig. 2) does not suggest any marked difference between the two classes of sites. To investigate this formally, we calculated the coefficient of variation (CV) in annual colony size for the 41 sites with ≥ 15 years of data, and plotted these coefficients in relation to the number of neighboring colony sites (Fig. 4). We used the CV to standardize our measure of size variability for colony sites that often differed widely in their mean colony sizes. Although the CVs for the 9 sites without any neighbors (mean CV = 1.3, SE = 0.4) did not differ significantly from those for the 32 sites with ≥ 1 neighboring colony (mean CV = 1.2, SE = 0.1; Mann-Whitney test, $U = 116$, $P = 0.38$), there was a significant positive correlation between the CV and the actual number of neighboring colonies when all sites (including neighborless colonies) were considered ($r_s = 0.36$, $P = 0.02$, $n = 41$; Fig. 4). Thus, colony sizes at sites with more neighbors tended to vary somewhat more from year to year than did the colony sizes at sites with few neighbors. However, the sites without any neighbors were not noticeably more consistent in size and themselves apparently did not contribute much to the significant statistical relationship in Figure 4.

COLONY-SIZE CORRELATIONS IN RELATION TO DISTANCE

For a subset of 22 sites, we examined whether the among-year correlation between colony size and the number of nests in neighboring colonies was related to the average distance of the neighboring sites (within the 2-km distance between sites). This addresses whether the extent of foraging-range overlap between sites might be important. We confined the analysis to sites with ≥ 15 years of data that had 2 ($n = 4$ colonies), 4 ($n = 7$), 5 ($n = 5$), and 7 ($n = 6$) neighboring sites. The direction and magnitude of the correlation coefficient did not vary significantly with the average distance to neighboring sites ($r_s = 0.27$, $P = 0.22$, $n = 22$; Fig. 5). This suggests

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FIGURE 2. Annual size (number of nests) of a Cliff Swallow colony site in relation to the total number of nests in neighboring colonies (within 2 km) that year, for 10 sites (a–j) with 15–17 years of data each. Each plotted point for a site represents a different year.

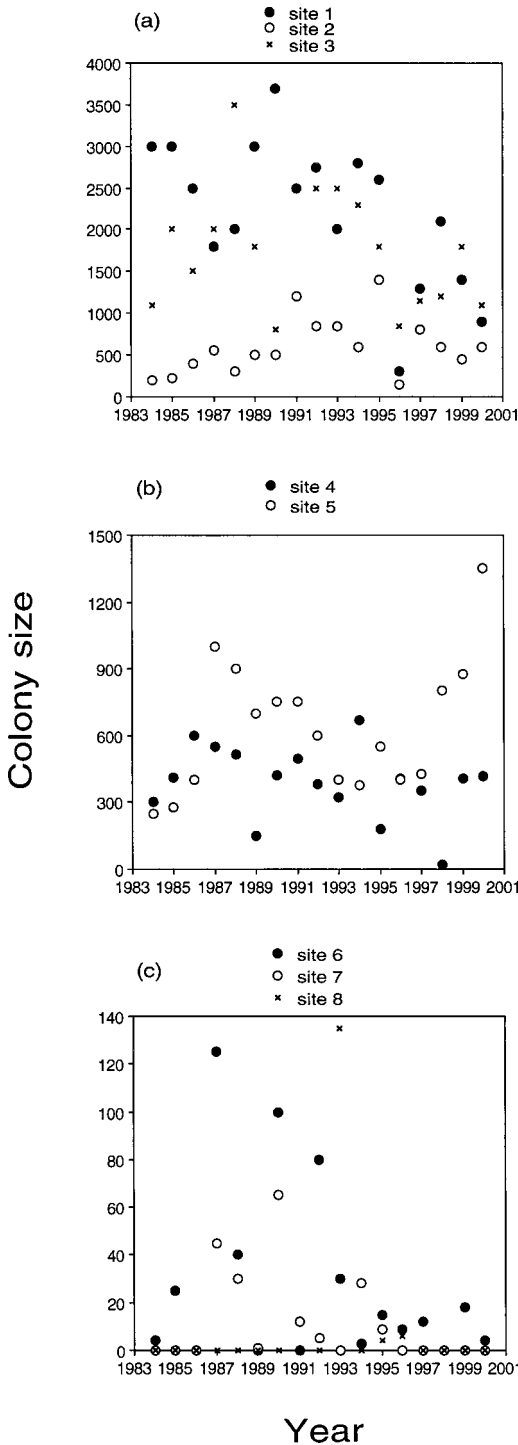


FIGURE 3. Annual size (number of nests) of eight Cliff Swallow colony sites that had no neighboring colonies (within 2 km), grouped roughly into sites that were usually (a) large, (b) medium, and (c) small in size.

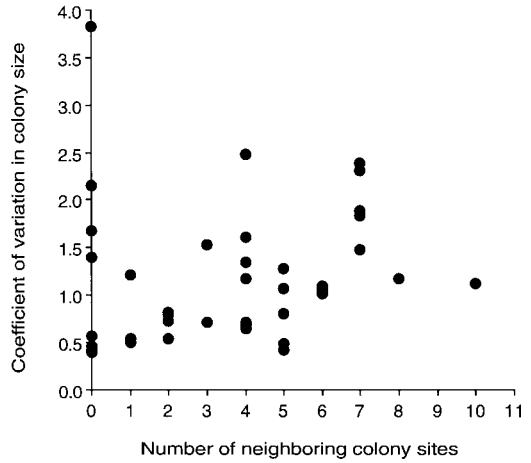


FIGURE 4. Coefficient of variation in annual Cliff Swallow colony size at a site in relation to the total number of neighboring colony sites (within 2 km). Only colonies with 15–17 years of size and usage data were included.

that the extent of overlap in foraging ranges was unlikely to have affected our conclusions based on simple presence or absence of overlap and that inclusion of distance (within the 2-km range) in the other analyses would not have yielded any additional insight.

DISCUSSION

We found only weak evidence that Cliff Swallow colony size at a site might have been influenced by competition for food from neighboring

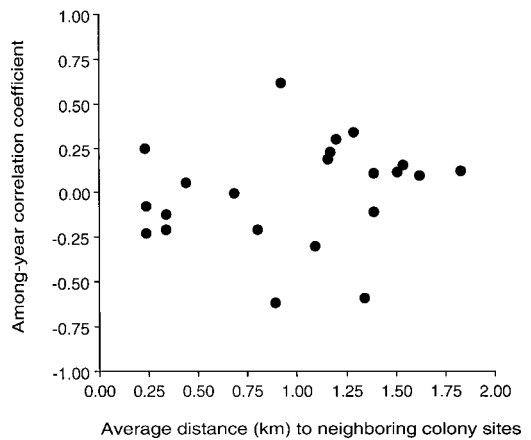


FIGURE 5. Among-year Spearman rank correlation coefficients (r_s) between colony size and the number of nests in neighboring colonies in relation to the average distance (km) to the neighboring colony sites.

colonies. As predicted by the intercolony-competition hypothesis, in some years there was a pattern of the largest colonies occurring in areas with limited foraging-range overlap from other sites, and some of the smaller colonies were ones that overlapped with neighboring sites containing many nests. Furthermore, annual variability in colony size seemed to increase as a site shared its foraging range with more neighbors. However, the statistical patterns across all analyses were weak, the among-year analyses within sites showed almost no evidence that intercolony competition influenced settlement decisions, and there were many small to medium-sized colonies that shared their foraging range with other small to medium-sized colonies. Thus, on balance, it appears that intercolony competition for food might be important for Cliff Swallows only in certain situations or at certain sites.

We have made the assumption in this study that foraging ranges of different colonies are homogeneous with respect to food availability and thus, if food competition occurs, the available food will be depleted as a direct function of the number of foragers within a foraging range. This was also implicitly assumed in the seabird studies of Furness and Birkhead (1984) and Lewis et al. (2001). However, if physical features of the foraging habitat cause heterogeneity in food availability, this alone could lead to some colonies being more strongly affected by competition from neighboring colony sites than others and perhaps account for some of the variation we observed among sites. Although the foraging habitat around Cliff Swallow colony sites does in fact differ as measured by general landscape features, these differences do not seem to be ones that reflect overall food availability (Brown et al. 2002). Given that we have not identified any systematic habitat-related influences on insect abundance around colony sites, our assumption in this paper that habitat does not influence food availability within foraging ranges seems justified.

For intercolony competition to be a determinant of colony size, the food resource must be to some degree limited and subject to depletion as increasing numbers of individuals use it in a given area (Cairns 1992). This appeared to be the case for the prey species taken by the four seabird species studied by Furness and Birkhead (1984), based on the strong negative correlations

between colony size and degree of foraging-range overlap by neighboring colonies that were reported (see also Lewis et al. 2001). That we found much weaker relationships for Cliff Swallows could be because their insect prey is abundant and generally unaffected by the number of foraging swallows in a local area. In particular, the Cliff Swallow colonies that showed positive among-year correlations between colony size and size of neighboring colonies imply that food is not limiting in some situations. Ainley et al. (1995) similarly interpreted the lack of a relationship (or in one species, the positive relationship) between colony size and the number of birds in neighboring sites in Antarctic penguins to reflect a superabundance of food within foraging ranges.

Another factor that could account for the weak relationships we found in Cliff Swallows is synchrony of settlement. The intercolony-competition hypothesis proposes that colony size is regulated by the presence of birds in neighboring sites that share the same feeding area. Thus, an incoming settler presumably assesses either the number of foraging conspecifics it encounters or prey availability directly. This works if the neighboring colonies are already established when new arrivals appear at a colony site and make their decision to stay or not. However, if colonies are founded simultaneously, birds may be settling at each before colony sizes are final and therefore before they can accurately know the degree of intercolony competition that results from neighboring sites. Once established (nests are built), due to the cost of relocating, individuals may be predisposed to remain even if they suffer food-related costs later. Cliff Swallows tend to establish colonies relatively synchronously. In 1997, for example, 60% of active colony sites first became active from 1–15 May. This synchronized settlement, coupled with the fact that birds continue to arrive at colony sites for two weeks or longer after the first birds settle (Brown and Brown 1996), may mean that incoming settlers are faced with considerable uncertainty as to the extent of intercolony competition that can be expected at any given site. Perhaps only birds that found the relatively few late-starting colonies in our study area (after colony sizes at most sites are definitively established) can use the degree of expected intercolony competition for food in making settlement decisions. The degree of intercolony synchrony

in colony establishment was not reported by Furness and Birkhead (1984), but their results would suggest that the synchrony was low, giving birds opportunities to make accurate assessments of the degree of intercolony competition that could be expected at different sites. Nevertheless, it seems likely that synchrony in colony establishment is a constraint that works in general against animals being able to use the degree of expected intercolony competition for food in making settlement decisions.

The variability among sites in the apparent degree to which intercolony competition influenced settlement decisions could also have been related to the extent of overlap in foraging ranges. Perhaps sites closer to each other, with greater degrees of overlap, were affected by their neighbors' colony sizes to a larger extent than were sites with more distant neighbors. However, this seems unlikely because we found no effect of linear distance to neighboring sites on the among-year correlations.

For intercolony competition for food to be a significant factor in making settlement decisions, the animals must not be constrained by the availability of nesting sites (Furness and Birkhead 1984, Cairns 1989). If breeding space is limited, particularly within sites, a colony may be small because the site cannot accommodate all potential settlers, not because of competition for food. This could conceivably generate the patterns we observed, accounting especially for cases of small colonies being associated only with other small neighboring colonies. While not negating the potential influence of intercolony competition, the effect of site limitation would prevent a clean test of the intercolony-competition hypothesis. We do not think this is an issue for Cliff Swallows, however, as colony size is not significantly correlated with the amount of physical nesting space available at colony sites (Brown and Brown 1996).

Cairns (1989) questioned Furness and Birkhead's (1984) hypothesis that intercolony competition for food could regulate colony size. Cairns suggested that most seabirds, including those studied by Furness and Birkhead (1984), occupy non-overlapping, exclusive foraging areas near their colonies and that travel distances dictate that birds not forage closer to other colonies than to their own. The zone of feeding habitat closer to a colony than to any neighboring colony was termed the colony's "hinter-

land" by Cairns (1989). If birds forage only within their hinterland and if colony size is determined by food availability, then colony size should be related to hinterland size (Cairns 1989). That this alternative hypothesis would be proposed reflects in part Furness and Birkhead's (1984) lack of information on where their birds actually foraged and thus whether their foraging ranges overlapped at all.

The hinterland hypothesis does not apply to Cliff Swallows for two reasons. First, we know from direct observations that birds from adjacent colonies often feed in the same areas and that foraging ranges of neighboring sites can indeed overlap substantially. Second, Cairns' (1989) rationale that colonies should forage exclusively in hinterlands requires that the food resource be distributed uniformly. Essentially, it is the same argument first made by Horn (1968), who showed that animals should travel relatively small distances centered around their nests whenever food is uniformly distributed. However, when food is spatiotemporally variable (as is the case for Cliff Swallows), larger foraging ranges will be required because at times food may be unavailable close to a colony but present near a neighboring colony. Thus, in these situations hinterlands themselves will vary in size as birds from adjacent colonies move back and forth, and consequently hinterland size per se probably provides relatively little predictive power. For these reasons, it seems that intercolony competition as originally envisioned by Furness and Birkhead (1984) is more applicable to Cliff Swallows than the hinterland model.

Although on balance we did not find strong evidence of intercolony competition for food in Cliff Swallows, we do not discount this entirely as a potential determinant of colony size. At certain sites, for example, the negative among-year correlations suggested that colony size was related to the number of birds at neighboring sites. Although a high degree of synchrony in colony establishment may prevent Cliff Swallows from routinely basing their settlement decisions on the degree of intercolony competition for food, this sort of competition could figure into site choices made by late-arriving, asynchronous individuals. In addition, even though intercolony competition may not always lead to significant food depletion, we do know that Cliff Swallows depress food availability around their colonies at times. Birds in larger colonies travel farther within

their foraging areas (Brown and Brown 1996), which is probably a manifestation of within-colony competition for the food closer to the colony, and suggests that between-colony competition could also occur.

Explaining the observed variation in colony size remains one of the most vexing problems in the study of animal spatial distribution in general and for Cliff Swallows in particular. We began this study hoping to gain some additional insight into why Cliff Swallow colonies vary so much in size, both within and between years. As illustrated by the sites with no overlapping neighbors, colony size at a site varies considerably from year to year even in the absence of any intercolony competition for food. Since we have not yet identified any strong physical (i.e., habitat-related) determinants of colony size, we return to our earlier conclusion that colony-size variation in Cliff Swallows is primarily socially based, with individuals specialized for large or small colonies forming and settling in colonies of those sizes (Brown and Brown 1996, 2000), perhaps through collective decision-making processes. Clearly, colony choice in Cliff Swallows is complex, with the process including genetic predispositions to certain group sizes, assessment of one's own and others' past reproductive success at a site, and attraction of naïve birds to conspecifics (Brown and Rannala 1995, Brown and Brown 1996, 2000, Brown et al. 2000). However, it also appears that colony size at times and at certain sites can be constrained by habitat diversity and its effects on insects (Brown et al. 2002) and perhaps by the distribution of potential competitors from adjacent colonies (this study). In light of this, we urge other studies of colonial birds not to ignore the potential effect of intercolony competition for food, especially when food resources are variable and if foraging-range overlap can be demonstrated. We still have too few data on intercolony competition to evaluate its role in the evolution of animal coloniality in general.

ACKNOWLEDGMENTS

We thank the 52 research assistants who have helped us in the field since 1982. The School of Biological Sciences at the University of Nebraska-Lincoln allowed use of the facilities at the Cedar Point Biological Station. For financial support, we thank the National Science Foundation (BSR-8407329, BSR-8600608, BSR-9001294, BSR-9015734, DEB-9224949, DEB-9496113, DEB-9613638), the Erna and Victor Hassel-

blad Foundation, the National Geographic Society (3244-85, 3996-89, 4545-91, 5469-95), the American Philosophical Society, Princeton University, the University of Tulsa, Yale University, the Cedar Point Biological Station, the Chapman Fund of the American Museum of Natural History, the National Academy of Sciences, Sigma Xi, and Alpha Chi.

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