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NEST PLACEMENT RELATIVE TO FOOD AND ITS INFLUENCE ON THE EVOLUTION OF AVIAN COLONIALITY

CHARLES R. BROWN,* MARY BOMBERGER BROWN,* AND ANTHONY R. IVES†‡

*Department of Biology, Yale University, P.O. Box 6666, New Haven, Connecticut 06511;
†Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195

Abstract.—A model proposed by Horn, in which he showed that animals can reduce their travel distances by nesting in the center of their foraging arena whenever food is unpredictable, is often cited as a potential cause of avian coloniality. We investigate to what degree the model may account for the evolution of colonial nesting in cliff swallows (*Hirundo pyrrhonota*) and other birds. Two critical assumptions of the model, that foraging arenas are externally bounded and that potential nesting sites are distributed uniformly, do not hold for cliff swallows. Consequently, the model cannot apply to cliff swallows or explain why they live colonially. Rigorous evaluation of these assumptions is necessary before testing the model for a given species because, as we show for swallows, the model's predictions can be upheld even when both assumptions are violated. Reduction in travel distance by nesting at a central site is probably a general result for any central place forager that exploits a spatiotemporally variable food source. This result per se does not mean that the geometrical model explains coloniality. Because the model's critical assumptions probably seldom hold for natural populations, the model is unlikely to explain the evolution of avian coloniality in general.

The adaptive significance of colonial nesting in birds has attracted considerable attention, and a variety of potential benefits have been hypothesized to explain avian coloniality. Some of these (e.g., predator avoidance and information sharing about food) have been examined in a number of species (reviewed in Wittenberger and Hunt 1985). However, the potential energetic advantages of coloniality that result from colony placement relative to food sources (Horn 1968) have received virtually no attention in field studies. Consequently, these considerations represent a gap in our understanding of how group living may have evolved (Wittenberger and Dollinger 1984; Wittenberger and Hunt 1985).

Nesting at a site that is located centrally with respect to food sources provides the opportunity to reduce the mean distance traveled between the nest and foraging locations. When many individuals from the same species minimize their travel distance in this way, a colony may form at the common, central site (Horn 1968). Horn's "geometrical model," as it was termed by Wittenberger and Hunt (1985), is often claimed to be a potentially important selective force favoring avian coloniality. The article containing this model (Horn 1968) has been cited over 200 times through 1988 (our tabulation from *Science Citation Index*). Yet, despite the con-

‡ Present address: Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706.

siderable interest that Horn's model has generated and the fact that it is now over 20 yr old, there exist no data for any species to evaluate its applicability, its predictions, or its overall importance (see Wittenberger and Hunt 1985). The main conclusion that follows from Horn's model is that animals that group their nests in colonies may at times realize considerable energetic savings over animals that spread their nests more uniformly over the active foraging arena.

The geometrical model has several underlying assumptions that must hold if it is to be applied successfully in nature. These assumptions have generally been ignored or overlooked, and consequently there has been confusion over when and how Horn's model may be applied to explain coloniality. Furthermore, it has not been emphasized that testing the model requires direct testing of all of its assumptions. To show that the prediction of the model is correct (i.e., that centrally nesting individuals have reduced travel distances), it is necessary to construct the hypothetical case where nests are dispersed throughout a foraging arena. All of the geometrical model's assumptions are used in constructing the hypothetical case, and therefore all assumptions must be tested directly. The existing confusion over the applicability of Horn's model to colonial animals has probably occurred in part because there are so few field data from natural populations that are relevant to either the model's assumptions or predictions.

Here we explore both the model's underlying assumptions and its predictions. We report data for colonial cliff swallows (*Hirundo pyrrhonota*) that are relevant to the geometrical model and examine to what degree the model may account for the evolution of coloniality in cliff swallows and colonial birds in general. Wittenberger and Dollinger (1984) specifically suggested cliff swallows as a species in which Horn's model might explain coloniality. Many of the potential costs and benefits of coloniality in cliff swallows have been studied at our research site in southwestern Nebraska (see, e.g., Brown 1984, 1986, 1988*a*; Brown and Brown 1986, 1987, 1988*a*, 1988*b*), but potential advantages described by Horn's (1968) model have not been previously addressed.

HORN'S MODEL

The model suggested by Horn (1968) shows that when food is uniformly distributed and continuously available, individuals may minimize their travel distances from the nest site to food by distributing nests evenly throughout the minimum arena in which foraging occurs. This allows individuals to take advantage of food resources in the immediate vicinity of the nest. With a uniform food distribution, a centrally located nesting site more than doubles average travel distance (Horn 1968). In contrast, when food is unpredictably available in time and space, individuals must forage throughout the entire region containing food rather than just locally around the nest. Consequently, a centrally located nesting site is most efficient, and dispersed nesting requires a 31% increase in average distance traveled to find food. Although the simple representation in which all foraging sites are used equally over time is most often associated with the model, Horn (1968) noted that it can be expanded to include variation in usage and thus weighting of different foraging sites (see also Wittenberger and Dollinger 1984). Such an expan-
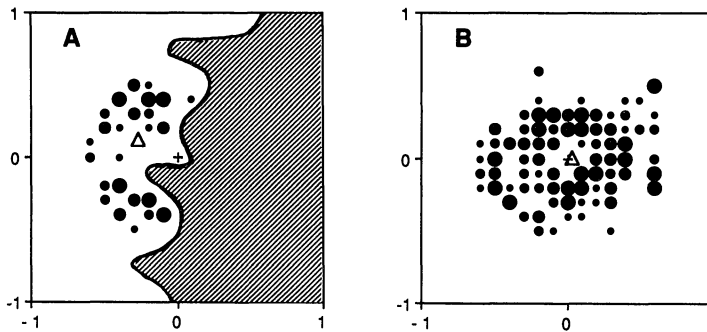
Fig. 1.—Foraging arenas for two cliff swallow colonies during nestling-feeding periods. Colony A consisted of 75 active nests, colony B of 750 nests. The actual colony location is shown by a plus sign, the foraging arena's center by a triangle, and foraging locations by dots. Relative size of dot indicates degree of usage of that foraging location (see Appendix). Scale of each is 2 km × 2 km. For colony A, the part of the foraging arena located over water is shown by shading.

sion may move the optimal nest position slightly but does not change the model's conclusions. Because Horn's model is most often used to explain coloniality, we focus here on the case in which nesting at a central point produces a smaller mean travel distance than dispersed nesting. Part of the geometrical model's appeal in explaining the evolution of coloniality is that it requires no initial aggregation of individuals before its advantages can manifest themselves (Horn 1968). Under the appropriate conditions, a solitarily nesting pair can receive the same travel benefits as a multipair colony at the same location.

APPLYING THE MODEL TO CLIFF SWALLOWS

Before the geometrical model can be examined, foraging positions of the individuals in a colony must be determined. This allows one to calculate the position of the colony site relative to presumed food sources and is necessary for later calculation of travel distances in any test of the model's predictions. We determined cliff swallow foraging locations and travel distances for birds occupying 11 different colony sites in our study area near Ogallala, Nebraska. Field methods of observing foraging birds and mathematical methods for mapping foraging arenas and calculating travel distances and the areas of foraging arenas are given in the Appendix.

Foraging Arenas and the Distribution of Colonies

Foraging locations and relative use of each location by the cliff swallows are plotted relative to the colony's location for two representative colonies of 75 and 750 nests in size (fig. 1). The center of each colony's foraging arena, that is, the point at which travel distances would be least, is also shown (fig. 1). The foraging arena of the colony depicted in figure 1A is characteristic in size and shape of those colonies located on cliff faces in our study area, and that in figure 1B is
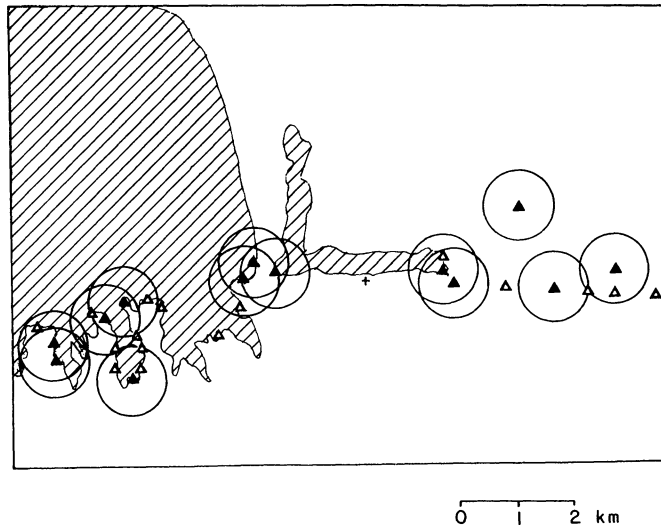
FIG. 2.—Distribution of active cliff swallow colonies (*filled triangles*) and unused colony sites (*open triangles*) in the vicinity of the Cedar Point Biological Station near Ogallala, Nebraska, in 1986. The circles are centered on each active site and indicate the foraging arenas of each colony. Unsuitable foraging habitat is indicated by shading; remaining space reflects appropriate foraging habitat. For locality reference, the location of the Cedar Point Biological Station is shown (*plus sign* in the center of the figure). Area shown is approximately 11 km × 6 km.

characteristic of colonies located on artificial nesting substrates such as bridges and highway culverts. The differences in shape of foraging arena and distribution of foragers between these sites resulted from the presence of a large lake adjacent to the cliff sites, which restricted foraging on one side of those colonies (cliff swallows in Nebraska feed mostly over upland areas and resort to feeding over water only during extremely poor weather). Artificial nesting sites were surrounded by uniform foraging habitat on all sides.

We plotted the spatial distribution of all active cliff swallow colonies and unused colony sites for a portion of our study area (fig. 2). For each active colony site, we have shown its foraging arena. Although areas of foraging arenas at different colonies varied (table 1), this variation was not great. For graphic purposes, in figure 2 we have used for all colonies the average arena area based on the 11 colonies studied in detail (1.25 km^2; table 1). This arena size is plotted for each active colony, including those for which actual arenas were not measured in the field (fig. 2). Unused sites were those that had been used at least once in previous years and that were thus judged at least grossly suitable. Habitat that was obviously unsuitable for cliff swallow foraging (i.e., lakes) is indicated by shading; all other habitat (in this case mostly uncultivated fields and pastures) was assumed to be at least minimally suitable for feeding. Data are shown for 1986, but plots for all other years are qualitatively similar.

Colony	Year	Colony Size	D_{col} (km)	D_{cen} (km)	Arena Area (km²)	D_{dis} (km)	Percentage Reduction in D_{dis} by Nesting Colonially
1	1986	10	.274	.248	.725	.405	32.3
2	1987	10	.254	.195	.523	.365	30.4
3	1986	75	.455	.261	1.423	.616	26.1
4	1986	100	.424	.303	1.422	.582	27.1
5	1985	456	.300	.199	.703	.424	29.2
6	1986	750	.329	.288	1.126	.502	34.5
7	1987	800	.355	.262	.972	.502	29.3
8	1986	1,100	.271	.225	.727	.406	33.2
9	1987	1,100	.384	.260	1.247	.565	32.0
10	1988	1,400	.638	.517	4.094	.955	33.2
11	1988	3,000	.443	.265	.809	.534	17.0
Average, all colonies		. . .	.375	.275	1.252	.532	29.5

NOTE.—One-way travel distance to observed foraging locations from the colony, D_{col}; from the foraging arena's center, D_{cen}; to observed foraging locations if nests were dispersed, D_{dis}.

Assumptions of the Model

The geometrical model makes two implicit assumptions that, although not mentioned in the original description (Horn 1968), must hold if the model is to be applied as originally developed. These are, first, that the foraging arena is externally bounded and beyond the boundary food is unavailable or not of sufficient quantity or quality to permit successful foraging; and, second, that nesting sites are uniformly distributed and virtually unlimited, which allows animals to choose freely whether to nest in dispersed fashion or colonially. In previous explorations of Horn's model, the latter assumption has been ignored, and the critical importance of the former assumption has not been emphasized (Wittenberger and Dollinger 1984; Wittenberger and Hunt 1985).

If a foraging arena is large and continuous, without boundaries and a center, the advantage of using a single centrally located site disappears (M. Rowe, cited in Wittenberger 1981; Wittenberger and Hunt 1985). If food is found over a wide area, the distances of foraging trips are limited only by the distances the birds can fly, and any one nest location is as good as another. Instead of aggregating in one large colony, birds may form smaller separate colonies or solitary nests at regular intervals throughout the habitat. This result is illustrated graphically in Wittenberger (1981) and Wittenberger and Hunt (1985). Horn's model implicitly assumes that the foraging arena has an edge and is circumscribed by external (topographic, habitat, or resource) features that are independent of any boundary caused solely by how far foragers are willing to fly. Furthermore, the arena must be small enough in size so that birds foraging from nesting sites in the arena's interior must often encounter the arena's boundary. Even if a potential arena is

bounded but the boundaries are farther from the colony than the birds normally fly to feed, clustering at a single site will not be favored because individuals can leave that site and move successively closer to the boundary (up to a distance not less than their maximum foraging range). With a bounded foraging arena sufficiently small in size and spatiotemporal variability in food, a colony located in the center of the arena is always favored (Horn 1968).

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. Animals' having this choice and their choosing the more favorable central option are the basis for the formation of colonies. If, however, nesting sites are scarce within the observed foraging arena, individuals are constrained to nest in particular places.

The spatial distributions of active cliff swallow colonies, unused colony sites, and foraging habitat (fig. 2) show that both of the model's assumptions are violated for cliff swallows. Some foraging arenas were located in uniform foraging habitat, and other identical habitat that appeared suitable for foraging abutted the observed foraging arenas on all sides. Although we have no direct measure of food abundance inside and outside the arenas, it seems unlikely that the arenas in these cases were in fact externally bounded. Exceptions to this did occur: foraging arenas of the colonies located on cliff sites were bounded on one side by a lake (fig. 2). But in most cases foraging arenas seemed to be bounded only by how far the birds were willing to fly to find food. The lack of external boundaries is illustrated by the overlapping of foraging arenas of nearby colonies (fig. 2).

The implicit assumption of uniformly distributed nesting sites was also clearly violated in cliff swallows (fig. 2). Although cliff swallow coloniality does not seem to be a direct result of limited nesting sites when the study area as a whole is considered (e.g., more unused sites than used sites exist in fig. 2), in all cases nesting sites were limited when their availability only within a given foraging arena was considered. Most colonies had less than three alternative nesting sites available within their foraging arena, and the maximum number of suitable alternative sites within any colony's foraging arena was four (fig. 2). Cliff swallows did not have the option of dispersing freely throughout their foraging arenas.

Since both assumptions of the geometrical model do not hold for cliff swallows (fig. 2), energetic advantages associated with nest placement relative to food are probably not the primary cause of coloniality in this species. We do not conclude, however, that foraging habitat necessarily has no influence on where cliff swallows choose to nest. To the degree that these birds have a choice in where to nest (fig. 2), conceivably individuals could assess the general quality of a foraging habitat and at times select among potential nesting sites the one closest or most central to the favored foraging arena. We do not know whether cliff swallows select colonies this way, and the issue is not likely to be resolved easily given the difficulties in interpreting foraging locations relative to nesting sites for species that forage in a central place fashion (see next section). But since foraging habitat in our study area in general appears to be relatively uniform among sites (fig. 2; C. and M. Brown, personal observations) with as yet no detectable differences among colonies in food resource availability (Brown 1988a), cliff swallow colony

selection based to any large degree on characteristics of local food resources seems unlikely at this point.

Predictions of the Model

Although the geometrical model cannot explain coloniality in cliff swallows, it might conceivably apply to certain species in restricted situations (see below). Because of this and also because its presumed potential as an explanation for avian coloniality has been discussed (Wittenberger and Dollinger 1984; Wittenberger and Hunt 1985), we wish here to make a general point about the model's predictions.

If the assumptions of an externally bounded foraging arena and uniformly distributed nesting sites are upheld, then a test of the geometrical model requires only measuring mean travel distances from the observed nesting site to observed foraging sites and comparing these to mean travel distances calculated for a hypothetical population that breeds dispersed throughout the observed foraging arena and forages in the same places. If observed travel distances are less than those calculated for the hypothetical population, individuals receive an energetic gain by breeding at the observed colony site. If observed travel distances are greater than those calculated for the hypothetical population, the geometrical model can be rejected. Rejection of the model for a colonial population in which the assumptions hold would mean that food resources are not spatiotemporally variable. For such a test, no other assumptions are necessary about resource distribution or relative usage of the foraging arena by individuals (cf. Wittenberger and Hunt 1985).

Individuals receive the reduction in travel distance only if food is unpredictably distributed in time and space (Horn 1968). This result, however, follows from central place foraging considerations. A circular foraging arena (which is what Horn's model essentially predicts) is most efficient for any individual forager that must regularly return to a fixed site such as a nest (Smith 1968; Hamilton and Watt 1970; Orians 1971; Covich 1976). Horn's (1968) model illustrates quantitatively that return to a central site is the most economical way to search for ephemeral prey for any central place forager. Wittenberger and Dollinger (1984) also illustrate quantitatively that travel distances can be reduced by nesting centrally whenever food is spatiotemporally variable. They demonstrate that nests can be displaced considerably from the central site and yet still receive reductions in travel distance. We wish to point out here, simply, that a reduction in travel distance for central nesters is an automatic consequence of an unpredictable food distribution. Therefore, any colonial species using a spatiotemporally variable food source and feeding in a central place fashion will show reduced travel distances (relative to a hypothetical dispersed population). Reduction in travel distance is likely to be a general phenomenon of limited predictive or explanatory power; Wittenberger and Dollinger's (1984) calculations illustrate how pervasive this result can be.

To illustrate this point for cliff swallows, we began by assuming that food resources only occurred where birds were actually observed foraging; this placed a boundary on the foraging arena. We also assumed that, hypothetically, birds

could nest uniformly throughout the foraging arena. Since the geometrical model assumes that spatiotemporal variability in food abundance forces each bird to feed throughout the entire foraging arena, all birds regardless of their nest's position must forage equally throughout all parts of the arena. For cliff swallows, spatiotemporal variability in insect abundance is probably almost this extreme. Our observations showed that at any one time most of the birds from a colony were using only one to three foraging locations, presumably because food abundance elsewhere in the foraging arena was low. Therefore, for the hypothetical case of uniform nest dispersion, we assumed that the location of a bird's nest did not affect its overall use of the foraging arena.

Under the assumptions above, it was possible to calculate the average travel distance for the hypothetical case of birds nesting dispersed throughout the foraging arena (see Appendix). To delimit the foraging arenas of colonies, we used a method of deriving the boundaries that weights all observations of foraging birds, rather than simply taking the perimeter that circumscribes all foraging observations. This method, which is discussed in greater detail in the Appendix, addresses cases in some colonies in which birds infrequently foraged far from the colony. Without weighting by the frequency of foraging at different locations, these distant feeding trips would unduly increase the perimeter of the primarily used foraging arena.

Table 1 compares the observed distance traveled for colonial individuals, D_{col}, with that expected for individuals nesting uniformly throughout the foraging arena, D_{dis}. As shown (table 1), the observed travel distance from colonies was an average 29.5% lower than that for the hypothetical case of dispersed nesting. The slight differences in the magnitude of the savings that birds achieved by colonial nesting among the different colony sites (table 1) probably reflect differences among sites in the relative degree of spatiotemporal variability in the colony's food or in how closely the colony's location corresponds to the center of the foraging arena.

This reduction in travel distance for colonial nesters results directly from the roughly circular shape of the colonies' foraging arenas (fig. 1) and the fact that cliff swallows in Nebraska feed on spatiotemporally variable prey (Brown 1985). We use this example (table 1) only to emphasize that the predictions of Horn's model may be supported even when its underlying assumptions are grossly violated. It is thus crucial to evaluate the model's assumptions before attempting any test of its predictions (cf. Wittenberger and Dollinger 1984).

THE EVOLUTION OF COLONIALITY

To what degree might Horn's (1968) hypothesis account generally for the evolution of avian coloniality? We know of no data for any species indicating that the assumptions of the geometrical model are strictly met. Some colonial species such as yellow-billed magpies (*Pica nuttalli*), fieldfares (*Turdus pilaris*), and Brewer's blackbirds (*Euphages cyanocephalus*) may come close to satisfying the assumption of uniformly distributed nesting sites, although even in these species nesting sites are probably not unlimited and distributed truly uniformly. Other colonial

species such as pelagic seabirds clearly violate this assumption since they often have only a single island within a local area on which to nest (Wittenberger and Hunt 1985). The necessary assumption of an externally bounded foraging arena probably does not occur regularly in any species and might be likely only for terrestrial colonial birds that occupy extremely small oceanic or habitat islands in which the island's borders serve to bound the foraging arena. Possible candidates for having a bounded foraging arena might include barn swallows (*Hirundo rustica*) nesting on small islands off the California coast (see Speich et al. 1986), orchard orioles (*Icterus spurious*) nesting in strips of riparian woodland in the Great Plains (C. Brown, personal observation), or fieldfares nesting in isolated, heterogeneous patches of birch forest in Sweden (see Wiklund 1982).

Because of its restrictive assumptions, the geometrical model probably seldom can account solely for the evolution of avian coloniality. We caution that it should not be viewed as an automatic potential advantage of coloniality. However, even for the many species that violate its assumptions to varying degrees, Horn's model is useful in underscoring the importance of colony location relative to food. Even if a species is not able to nest uniformly throughout an unbounded foraging arena, in most cases some alternative nesting sites do exist in sufficient quantity for either the entire colony to relocate or for individuals who choose to leave the colony.

What are the energetic consequences of nesting at the observed colony site versus at all other possible sites? Horn's basic approach could perhaps be modified to specific situations in which the distribution of alternative nesting sites is known. Whether travel distances are reduced at the observed colony site relative to the other possibilities could augment the other benefits of nesting in a colony at that site (such as enhanced predator avoidance or information sharing). Indeed, one of the strengths of Horn's model is that it potentially can explain initial aggregation of nests at a relatively centralized location for certain species (e.g., blackbirds), a difficult task for other evolutionary scenarios of coloniality (see Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990). The geometrical model merits further empirical study, but its limitations in applicability should be clearly recognized.

APPENDIX

OBSERVATION AND MAPPING METHODS

OBSERVING FORAGING GROUPS

Most cliff swallow colonies within the study area were located in open terrain with unobstructed views of the surrounding fields for distances of several kilometers from the colony sites (Brown 1986, 1988*a*). Colonies studied permitted level views of the nearby terrain on all sides. Cliff swallows typically feed relatively high above the ground (5–20 m), often in well-defined groups, which enabled us to see them with binoculars at virtually any location (Brown 1988*b*).

Surveys of foraging birds' positions were made at successive 10-min intervals for continuous periods of 1.5–4.0 h/d, in both mornings and afternoons. The observer was positioned at the colony site, usually sitting above the nests on either a road surface (e.g., in the case of culvert colonies) or the top of the cliff (in the case of colonies located on natural sites). The surrounding fields were scanned 360° around the colony. When a foraging group or solitarily foraging bird was spotted, the compass direction, approximate foraging group size, and the birds' distance from a nearby landmark of known distance from the colony were recorded. Landmarks consisted of a wide variety of stationary objects for which linear distances from the colony could be measured (e.g., stop signs, telephone poles, road intersections, irregularities of a creek bank, sandbars). For groups that were far from any known landmark, their approximate positions were determined by triangulation using known distances. All observations at all sites were made by one observer only (M.B.B.). To check the accuracy of the estimated group positions, at one site another observer (C.R.B.) independently estimated all group's positions. Estimates from M.B.B. and C.R.B. never differed by more than 20 m and usually did not differ at all; thus, we considered group positions accurate to 20 m. If a foraging group was large and relatively spread out, we used the compass heading and distance of the group's center as its position. Surveys of all foragers around the colony could be accomplished within 2–3 min, so each survey was almost an instantaneous record of where all foraging was occurring at that time. Total days on which observations were made at each colony ranged from 7 to 11.

Cliff swallows were scored as foragers only if they were actively feeding at the time of the scan. Foraging birds can be easily identified by their characteristic twisting and turning movements as they pursue prey (Brown 1985, 1988*b*). Birds that were commuting between the colony and the foraging sites were not included. Commuting birds generally fly in straight lines without stopping or turning and are easily recognizable. Swallows apparently rarely if ever forage during these straight-line flights; this was known because actual prey capture attempts by cliff swallows are obvious (see Brown 1988*b*), and we did not see any by commuting birds.

All observations were made during relatively warm, sunny weather when birds fed at altitudes of at least 5 m, which enabled us to see them easily. During occasional cloudy, cool, or rainy weather, cliff swallows fed low over the grass and were hard to see. Thus, for the sake of accuracy, observations were not made during these periods. This type of weather occurred on less than 10% of days during the season over which we observed colonies. Observations were made at each site on days relatively late in the nesting season (mid-June to mid-July) when over half of all birds in the colony were feeding nestlings and foraging activity was at a peak.

Using binoculars, we could easily see birds up to a radius of at least 1.5 km from each site, but cliff swallows rarely were seen foraging more than 1 km from their colony. Because of the extremely high visibility and openness of the terrain, we are confident that we did not routinely overlook birds at greater distances from the colony. The total number of foraging birds on any given scan was always consistent with the number of birds present in the colony as evidenced by colony size (number of nests). Thus, our surveys of foragers probably did not include large numbers of wandering birds that did not live at the colony from which they were seen. When a colony decreased in size through fledging of nestlings, the numbers of nearby foragers also declined. Furthermore, all colonies chosen for study (except one) were separated by at least 3 km from the nearest active neighboring colony.

This meant that our counts of foragers probably did not include birds from neighboring sites, since swallows usually seemed unwilling to fly more than 1 km from their colony to forage. When one of the colonies used in this study was abandoned by all residents late in the year (presumably due to severe ectoparasite infestations and not to lack of food), its foraging arena was completely deserted even though a colony 3 km away was still active and birds from it conceivably could have fed in the abandoned colony's arena. For these reasons, our map of a colony's foraging arena likely reflected only the foraging activities of that colony's residents.

MAPPING FORAGING ARENAS

We first constructed maps of each colony's foraging arena by plotting the average number of birds recorded at each location around the colony. To do this, we divided the area surrounding the colony into a grid of points placed at 20-m intervals, since 20 m was the resolution of the observations on bird foraging locations. For notation in later mathematical equations, let each point on the grid be denoted (x_i, y_i) where x increases from west to east and y increases from south to north. The colony is assigned the coordinate $(0, 0)$. For each day of sampling at a given colony, the scans of the foraging arena were pooled to give the number of birds seen at each point on the 20-m grid; let the daily average number of birds seen per 10-min sample at the point (x_i, y_i) be denoted b_i. Note that b_i will equal zero if no bird is seen at (x_i, y_i), as is frequently the case. The b_i's from each day were then combined to give B_i, the number of birds seen per 10-min sample at point (x_i, y_i) averaged across all days of observation. Because the b_i's represent the average number of birds seen per sample, the calculation of B_i weights all days equally despite variations in the numbers of 10-min scans taken on different days.

As examples, figure 1 shows for two sites the distribution of birds foraging around the colony, that is, the B_i's. For the graphical presentation, birds have been grouped onto a grid with points at 100-m intervals. The sizes of the black dots in figure 1 represent the relative numbers of birds at each point. For each colony there are equal numbers of four sizes of black dots, the largest dot size corresponding to the largest 25% of the B_i's for that colony and the three smaller dot sizes assigned to the smaller quartile ranges of B_i's.

The data used to derive figure 1 were analyzed to give four different measures that are useful in describing swallow foraging: (1) the average distance traveled from the colony to foraging locations, (2) the center of the foraging arena, (3) the area of the foraging arena, and (4) the average distance that birds would travel if all nests were dispersed uniformly throughout the foraging arena.

Average Travel Distance

We assume that the number of trips that birds make to a particular foraging location is proportional to the total number of birds observed. This assumption is valid because group size does not affect the duration that a foraging group remains at a particular location (C. Brown and M. Brown, unpublished data). If $B_s = \Sigma_{i=1}^{N} B_i$, then (B_i/B_s) is the fraction of trips made to location (x_i, y_i) over the period of observation, and the average one-way distance traveled from the colony to foraging locations, D_{col}, is given by

$$D_{col} = \sum_{i=1}^{N} \sqrt{x_i^2 + y_i^2} \, (B_i/B_s).$$ (A1)

Center of Foraging Arena

We define the center of the foraging arena as that point at which the average distance to observed foraging locations is minimized. The average distance from any point (x, y) to the foraging locations, denoted $D(x, y)$, is given by

$$D(x, y) = \sum_{i=1}^{N} \sqrt{(x - x_i)^2 + (y - y_i)^2} \, (B_i/B_s).$$ (A2)

Let $(x_\triangle, y_\triangle)$ be that point that minimizes $D(x, y)$, and denote $D(x_\triangle, y_\triangle)$ as D_{cen}. Because there is no explicit formula for $(x_\triangle, y_\triangle)$, it must be calculated implicitly from equation (A2) using numerical methods.

Area of Foraging Arena

Calculating the area of the foraging arena requires first defining where the boundaries of the arena lie. Because there were no abrupt geographical boundaries of the foraging arenas, the boundaries must be determined from the observed foraging patterns. The boundary could be defined as the smallest ellipse, or the smallest polygon, that circumscribes all foraging observations. However, this definition can give misleading results because it does not distinguish distant foraging locations that are used rarely from those locations that are used more frequently. Therefore, the boundaries may not reflect the average travel distance that birds must fly when foraging.

Instead of using the most distant foraging locations to determine the boundary of the foraging arena, we derived a method for finding the boundary that uses all observations of foraging. We define the boundary of the foraging arena as that line along which every point is on average 2 D_{cen} from all of the foraging locations. That is, the boundary is the line of points (x_b, y_b) such that

$$2 D_{cen} = \sum_{i=1}^{N} \sqrt{(x_b - x_i)^2 + (y_b - y_i)^2} \, (B_i/B_s) . \tag{A3}$$

This definition has the advantage that the average radius of the foraging arena will vary roughly proportionally with the average distance from the center of the foraging arena to the foraging locations. Distant foraging locations that are rarely used and therefore contribute little to the average distance from the arena center may lie outside the boundary.

For example, consider three hypothetical cases that illustrate extreme examples of how foraging birds may be distributed in space; these cases demonstrate some properties of the method we use to define the boundary of a foraging arena. In case A, all birds forage exactly 0.5 km from the colony, so the average one-way travel distance to foraging locations is 0.5 km. In cases B and C, the average one-way travel distances are also 0.5 km; but in case B birds forage uniformly at all distances from the colony, and in case C birds forage with greater frequency close to the colony.

The probability density functions for bird foraging locations depending on the distance from the colony, r, are A, $1/\pi$ for $r = 0.5$, 0 elsewhere; B, $16/(9\pi)$ for $r \leq 0.75$; and C, $(3/\pi)(1 - r)$ for $r \leq 1$. The values of the radii of the foraging arena's boundaries are A, 0.93 km; B, 0.92 km; and C, 0.91 km. Although the radii are not equal, they are close, which shows that they are more strongly determined by mean travel distance (which is the same for each case) than the outermost foraging locations.

After determining the boundary of a foraging arena, we directly calculated the area of the arena. If $R(\theta)$ is the radius of the foraging arena at any angle θ from the calculated center of the arena (eq. [A2]), then in polar coordinates the area of the arena, A, is

$$A = \frac{1}{2} \int_0^{2\pi} R^2(\theta) d\theta . \tag{A4}$$

Average Travel Distance from Dispersed Nests

To consider the hypothetical case of uniformly dispersed nests, assume that a bird whose nest is located within the arena uses each of the foraging locations in the same proportion as observed in the field (e.g., fig. 1). Then the average one-way travel distance for all birds with nests dispersed in the foraging arena, D_{dis}, is given in polar coordinates by

$$D_{dis} = \int_0^{2\pi} \int_0^{R(\theta)} r \sum_{i=1}^{N} \sqrt{(r\cos \theta - x_i)^2 + (r\sin \theta - y_i)^2} \, (B_i/B_s) dr d\theta . \tag{A5}$$

Programs for the data manipulations and computations used in equations (A1)–(A5) are available from A.R.I. upon request.

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