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Cliff Swallow Colonies as Information Centers

CHARLES R. BROWN*

Colonies of cliff swallows (*Aves: Hirundo pyrrhonota*) appear to be information centers in which colony residents acquire information on the location of food sources. Individuals that have been unsuccessful on a foraging trip return to the colony, locate a successful forager, and follow that individual to a food source. Individuals often follow, and are followed by, their neighbors within the colony, possibly because neighbors can observe foraging success through food brought back to nestlings. All individuals are equally likely to follow others or be followed, and thus all individuals benefit from opportunities to receive information.

ONE MAJOR ADVANTAGE OF LIVING in a group is the opportunity provided to observe other group members find food (1). Transfer of information about the location and quality of food often occurs at a fixed location such as a breeding colony, and a colony is considered an "information center" in such cases (2, 3). The best examples of information centers occur in social insects, especially honey bees (*Apis* spp.), where individuals (that are often related) inform each other about food location and quality (4). However, few if any unequivocal examples of information centers have been found among nonhuman vertebrates (3, 5). Breeding colonies and communal roosts of birds are prime candidates in which to expect the evolution of information centers (2, 6). I report a case of an information center in a colonial vertebrate, the cliff swallow (*Hirundo pyrrhonota*).

Cliff swallows are small migratory passerines that nest in colonies throughout much of western North America. The birds arrive in the southern and coastal parts of their breeding range in March and in most other areas by early May. Most cliff swallows leave North America in August and September for their wintering range, which extends from southern Brazil to Argentina and Chile (7). The birds build gourd-shaped nests out of mud, and the nests are fastened under-

neath overhanging rock ledges on the sides of cliffs and canyons or, more recently, on artificial structures such as bridges and highway culverts. These birds feed exclusively on insects caught in flight. Cliff swallows feed, preen, gather mud for their nests, and migrate in synchronized groups (8, 9). There is no evidence that cliff swallow colonies are composed of close genetic relatives (10), and thus kin selection is probably unimportant in the evolution of their social behavior. Nesting within each colony is highly synchronous, and these usually monogamous birds typically raise a single brood (8-11).

This study was done in Keith and Garden counties, Nebraska, from May to August, 1982 through 1985. In this area, cliff swallows nest on natural cliff sites, bridges, culverts, and occasionally buildings. My assistants and I studied 167 cliff swallow colonies totaling 53,308 nests (9). Colony size ranged from 1 to 3000 nests (mean, 319.2; SD, 522.0).

For an animal colony to be an information center, individuals living there that have recently been unsuccessful at finding food either (i) must be informed of food sources by successful individuals through active signals (such as a language or a form of chemical communication) or (ii) must recognize successful individuals on the basis of appearance or behavior and follow them to food

sources. I focus on the second alternative because there is no evidence that cliff swallows (or any other birds) communicate about food sources with language or pheromones (12).

Cliff swallows feed on localized concentrations of aerial insects that occur unpredictably in both space and time (9). These concentrations are caused principally by localized convection currents that create high densities of insects within each patch. The birds also feed on insects that temporarily congregate in mating swarms and mass emergences. A patch of insects can often support more than 500 foraging swallows, but patches seldom last longer than 20 to 30 minutes, after which time the birds must locate another one (9). Thus, to continuously receive information on the location of a current foraging location is important to an individual in maintaining a high level of foraging efficiency. We discovered that when an individual cliff swallow is naïve about the present location of a food resource, that individual follows a knowledgeable neighbor from the colony to the food resource.

When feeding nestlings, cliff swallows in all colonies larger than ten nests clustered their departures from the nests (9). Clustered departures usually occurred as one individual followed another one away from the colony. We examined whether the birds that left together then fed together. Our study colonies were surrounded by treeless, open terrain, making it possible to observe with binoculars all foraging by colony residents. At two colonies, we visually tracked departing birds and kept them in sight until they reached a foraging location and began catching insects (13), or until members of the group drifted apart before ever starting

Department of Biology, Princeton University, Princeton, NJ 08544.

* Present address: Department of Biology, Yale University, New Haven, CT 06511.

to forage. We thus knew how many birds that departed together also subsequently foraged together. A departing group was defined as all birds departing from a colony within 5 seconds of each other (14). We scored group size upon departure from the colony and the subsequent group size when those birds began foraging (Fig. 1) (15). Most birds that departed together (that is, followed one another) also foraged together (Fig. 1).

Tendencies for individuals to follow other cliff swallows or to be followed were influenced by foraging success. At two colonies of 450 and 800 nests, we observed birds feeding nestlings and recorded whether nest owners arrived at nests with food and fed nestlings or whether they arrived without food. Birds with food were obvious: insects could be seen in bills or bulging in throats as birds perched on the outside of nests, and when birds fed nestlings they characteristically rocked their bodies back and forth in placing the food boluses into the nestlings' mouths (16). Birds arriving without food simply clung to the nest entrance. After scoring whether a parent had food or not, we recorded whether it followed another

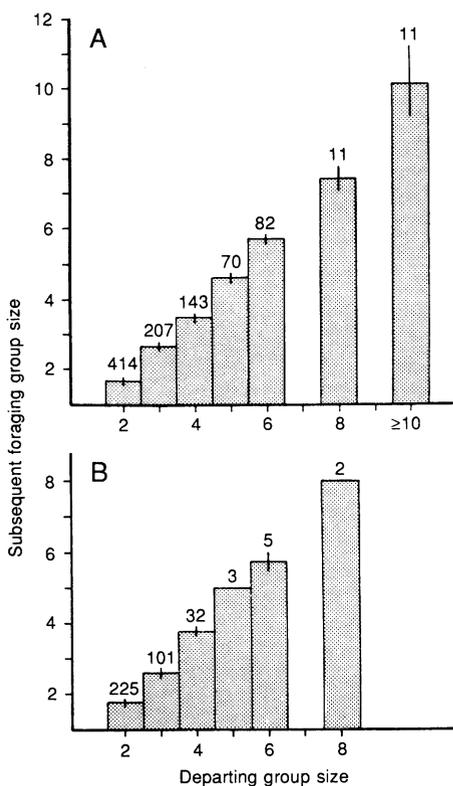


Fig. 1. Subsequent foraging group sizes of cliff swallow groups departing from (A) a 165-nest colony and (B) a 13-nest colony. Mean (± 1 SE) shown for each departing group size. Total groups observed for each departing group size are shown above error bars. Close agreement between departing group sizes and subsequent foraging group sizes indicates that most birds departing from a colony together foraged together.

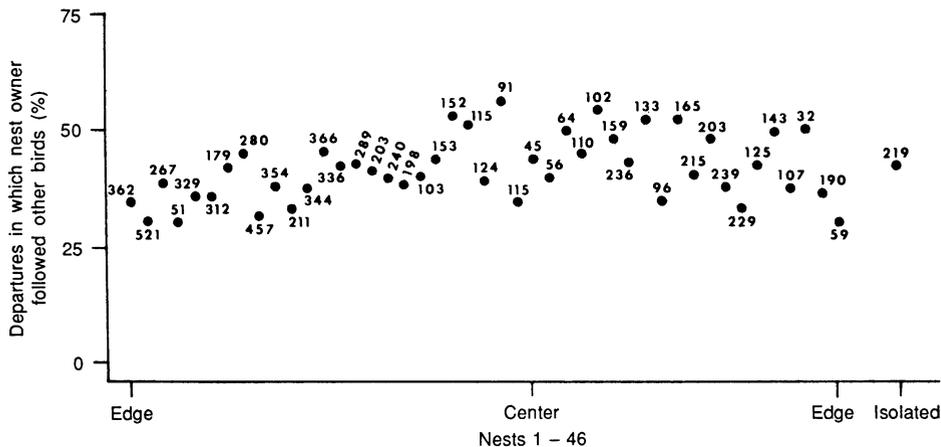


Fig. 2. Percentage of departures in which nest owners followed another bird or birds at 46 cliff swallow nests. Relative position of each nest with respect to the other 45 is shown. Each circle represents one nest and the total number of departures at each nest is shown.

bird, was followed by another bird, or left alone on its next foraging trip (17). We recorded data for 4943 departures of birds for whom we knew the recent foraging success.

Individuals that had been unsuccessful on a previous foraging trip were more likely to follow other birds than were ones that had been successful (Table 1). Probably not all birds that returned without food had been unsuccessful; at times nestlings might have been satiated. These cases could account for the (relatively few) individuals returning without food but who did not follow others on the next trip (Table 1) (18). Individuals that had been successful on their previous foraging trip were more likely to be followed on their next trip than were individuals that had been unsuccessful on their previous foraging trip (Table 1). The number of successful birds not followed probably reflects an absence of unsuccessful birds at nearby nests at the time that these successful individuals departed. An unsuccessful individual was unlikely to be followed at any time (Table 1).

Since cliff swallows carrying food back to their nests were obvious to humans, presumably such individuals are obvious to other cliff swallows. Carrying food may be a reliable signal that an individual knows the location of a concentration of prey. If so, birds might more easily observe and follow their closest neighbors than distant neighbors. At 46 focal nests in a 165-nest colony, each time a color-marked nest owner followed another bird from the colony, we recorded the identity of the follower and the bird being followed. We observed 3146 followings, and divided these into ones directed at a nest owner's mate and at nest owners living one to five nests away, six to ten nests away, and more than ten nests away. We calculated the number of times

those owners should follow mates and neighbors if all birds were followed equally (19). Individuals clearly preferentially followed neighbors one to ten nests away and especially those within a five-nest distance (Table 2). However, followings were not directed exclusively at close neighbors; dis-

Table 1. Whether success on the previous foraging trip influenced whether birds followed or did not follow others on the subsequent trip, and whether success on the previous foraging trip influenced whether birds were followed by others or were not followed by others on the subsequent trip.

Subsequent trip	Previous trip	
	Successful	Unsuccessful
Followed	524	1355
Did not follow	2610	454
	$\chi^2(1) = 1647.6$ ($P < 0.001$)	
Was followed	1378	172
Was not followed	1756	1637
	$\chi^2(1) = 632.8$ ($P < 0.001$)	

Table 2. Number of times nest owners of 46 nests followed other individuals during feeding of nestlings in a Nebraska cliff swallow colony.

Action	Observed	Expected*
Nest owner followed mate	88	29
Nest owner followed owner 1 to 5 nests away	676	191
Nest owner followed owner 6 to 10 nests away	294	162
Nest owner followed owner >10 nests away	2088	2941
	$\chi^2(3) = 1706.5$ ($P < 0.001$)	

*If followings are equally directed toward all birds.

tant neighbors were also followed. Mates followed mates more often than expected if followings were random (Table 2). In addition to recognizing successful neighbors by the food in their bills, unsuccessful foragers might also cue on birds that depart the colony in rapid, direct flight (20). Direct flight patterns probably indicate a bird's movement to a foraging location and would enable an individual (in the absence of any information from its close neighbors) to gain information when even a distant neighbor departs from the colony.

For an information center to evolve, the relative success of different individuals must change regularly (21). Otherwise, consistently successful individuals gain nothing by nesting in colonies. We examined whether tendencies to follow others or be followed (that is, foraging success) varied among the residents of a colony. We scored 9077 departures of the color-marked nest owners in the 165-nest colony. For each nest we examined the percentage of departures in which nest owners followed other birds, were followed by others, or left alone (22) (Fig. 2). There were few differences among nests in birds' tendencies to follow other individuals. Virtually all birds were likely to follow others about 40% of the time (Fig. 2). Similar consistencies were found among all birds in tendencies to be followed by others and to leave alone (9). Thus, no birds were mainly followers, mainly leaders, or mainly solitary foragers, meaning that all colony members benefited about equally from the opportunities to receive information.

Taken together the data provide evidence for the existence of information centers in cliff swallow colonies. There was no evidence that birds attempted to disguise their foraging success in any way or to discourage other individuals from following them. The concentrations of insects at a foraging site are so dense that recruitment of additional foraging swallows probably does not affect an individual's harvest and thus there is no cost to being followed (23). Individual swallows also probably are selected to exploit each patch as quickly as possible since the patch may disappear in 20 to 30 minutes when convection at that spot ceases, and having to take circuitous routes to and from

the foraging area and colony to elude potential followers would waste time and impair a forager's ability to efficiently exploit a patch.

How are foraging locations discovered initially if the birds' principal foraging strategy is to recruit to discovered patches? The answer is not clear, but may be related to the observation that at any given time some individuals are foraging alone. A bird (usually after a previously successful foraging trip) departs alone about 20% of the time (9); these birds may be responsible for discovering many of the food sources. Discovery of new food sources is influenced by the size of a cliff swallow colony; how colony size affects the efficiency of an information center remains to be explored.

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12. Cliff swallows have a limited vocal repertoire [see D. E. Samuel, *Auk* 88, 839 (1971)]; C. R. Brown, *Southwest. Nat.* 30, 325 (1985) and at present there is no good evidence that any of their four major types of vocalizations are used as food-finding signals.
13. Foraging cliff swallows show characteristic abrupt twists and turns when pursuing insect prey. A bird flies on a level course until it spots an insect and then makes a sudden turn up or to either side to catch the insect. Once the insect is caught, a swallow slows, flares its tail (as a brake), then returns to its original altitude and resumes flying a level course. By observing birds catching insects, we verified that these behaviors do signal prey captures. Since the birds usually fed in well-defined groups, an individual's joining of a group that was already present in the foraging area was another cue that it had reached a foraging site.
14. Any designation of a departing "group" is to some degree arbitrary. We selected 5 seconds because we observed that birds that departed within 5 seconds of each other usually traveled together for at least 100 m from the colony. Birds whose departures were separated by more than 5 seconds often went in different directions. Further, cliff swallows can fly a considerable distance in 5 seconds, suggesting that individuals who departed more than 5 seconds apart might not have any opportunity to maintain visual contact.
15. Data were collected on 1317 groups ranging in size from 2 to 22 birds. For two-bird groups in which individuals separated, the subsequent foraging "group" size was one bird.
16. We collected these data only when birds were feeding large nestlings, at which time the nestlings effectively blocked the entrance to the nest and parents fed them without entering the nest. If a parent completely entered a nest and passed out of our sight, no data were collected.
17. Criteria for whether a bird followed another or was followed by another was a departure within 5 seconds (14) of the other individual and in the same direction, traveling together for at least 50 m from the colony. Individuals who left the colony behind others usually stayed behind them all the way to the foraging locations; thus, leader and follower status upon leaving the colony was maintained.
18. During the period in which these observations were made, birds were foraging almost exclusively and continuously; there was no indication that nest owners scored as unsuccessful were engaged in any nonforaging activities.
19. This expected distribution was the total number of followings at each focal nest, divided by the number of nests in the colony (165), giving the number of times an owner from any one nest was followed if followings were equally distributed. Expected numbers for 1-5 and 6-10 nest categories differ (Table 2) because some nests were located on the edges of the colony and did not have as many neighboring nests on both sides as did other nests.
20. Birds departing "purposefully" (2).
21. D. I. Rubenstein, R. J. Barnett, R. S. Ridgely, P. H. Klopfer, *Ibis* 119, 10 (1977); J. F. Wittenberger and G. L. Hunt, Jr., in *Avian Biology*, D. S. Farner and J. R. King, Eds. (Academic Press, New York, 1985), vol. 8, pp. 1-78. Each individual must be at times both a "producer" and a "scrounger" [sensu C. J. Barnard and R. M. Sibly, *Anim. Behav.* 29, 543 (1981)].
22. It was often difficult to identify specific color-marked members of a pair as they quickly arrived, entered, and departed from their enclosed nests. For this reason, both owners at a nest were combined for this analysis.
23. There is no evidence that foraging socially in cliff swallows is any form of antipredator behavior. Predation on adult birds in foraging flocks has never been observed in our study area.
24. I thank Mary Bomberger Brown for data collection; C. Boersma, C. Brashers, K. Brown, R. Budelsky, L. Doss, L. Jackson, D. Johnson, K. Miller, and T. Scarlett for field assistance; J. Janovy, Jr., for use of facilities at the Cedar Point Biological Station; and R. Brown, K. Brown, J. Hoogland, A. Ives, S. Robinson, D. Rubenstein, T. Seeley, B. Stutchbury, and D. Wilcove for other assistance. Supported by an NSF Predoctoral Fellowship and a Dissertation Improvement Grant, Princeton and Yale universities, the Chapman Fund of the American Museum of Natural History, the Bache Fund of the National Academy of Sciences, Sigma Xi, and Alpha Chi.

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