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EVIDENCE THAT BANK SWALLOW COLONIES DO NOT FUNCTION AS INFORMATION CENTERS[1]

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A benefit of colonial breeding may be that colonies act as information centers, where colony members improve their foraging efficiency through transfer of information at the colony about the location and quality of food resources (Ward and Zahavi 1973). For a colony to be an information center, birds must both recognize successful foragers, and then use them to locate the source of the food (Bayer 1982, Brown 1986). The best examples of bird colonies functioning as information centers are the Cliff Swallow (*Hirundo pyrrhonota*) (Brown 1986, 1988b), and Osprey (*Pandion haliaetus*) (Greene 1987).

This study examines whether information centers occur in colonies of the Bank Swallow (*Riparia riparia*), a colonial passerine found throughout much of North America. Information centers have been proposed as a benefit of group living in Bank Swallows (Emlen and Demong 1975). However, Hoogland and Sherman (1976) contended that social foraging benefits were not important in Bank Swallow colonies.

This study was conducted in Dickinson County, Iowa, from May to July 1987. In this area Bank Swallows nest primarily in sand and gravel pits, but also dig burrows along river banks. I focused my observations on three gravel pit colonies located near the town of Milford, Iowa. The colonies were about 1 km apart and were in open habitat with adjacent agricultural fields, and streams within 200 m of each colony. The contents of all accessible nest burrows were inspected several times per week using a tube with a mirror and light mounted at the distal end (Demong and Emlen 1975). Observations of foraging behavior were made in June and early July, when most (60%) colony members had nestlings. Colony size was defined as the total number of nests which had eggs or nestlings during the period of these observations (5 June to 10 July), and the three colonies studied had 26, 32, and 52 breeding pairs.

If colonies function as information centers, and successful foragers are followed back to the food source, then individuals that depart from the colony should often be followed by other colony members. In Bank Swallows, males mate guard intensely when their mate is fertile, and mate-guarding pairs are often followed from the colony by other birds (Beecher and Beecher 1979). These sexual chases are likely unrelated to improving foraging efficiency. Following behavior as a result of guarding and chasing fertile females is not likely represented in these data, because only 20% of the pairs laid eggs any time during the period of these observations. Furthermore, cases where two birds departed from a burrow in close succession (i.e., mate guarding), were excluded from the analyses.

To determine whether Bank Swallows follow each other away from the colony, I conducted 1-hr watches between 08:00 and 16:00, and I sampled all three colonies. When a single bird departed from its burrow, I recorded the group size in which that bird left the colony. Departing group size was defined as the number of birds (including the lead bird) leaving in the same direction (no greater than about a 10° angle from the focal bird) within 5 sec of each other (Brown 1986), such that a lead bird was no greater than 50 m ahead of other members of the group. Only those birds that stayed together over a distance of at least 30 m from the colony were considered a departing group. Distances were estimated from landmarks of known distance from the colony. A total of 69 hr of observation over 23 days resulted in observations of 1,851 departures. For each colony, Bank Swallows departed in groups in less than 15% of the departures (Table 1). This contrasts with Cliff Swallows, where 34% (169/497) of departures in a 13-nest colony were in groups (Brown 1988b).

If information transfer about the location of food occurs, then birds should preferentially follow previously successful foragers, but not unsuccessful foragers. Birds that return with food and feed their nestlings at the burrow entrance, presumably in clear view of other colony members, are known to be successful foragers (Brown 1986). When Bank Swallow nestlings reach an age of 18 days, they often remain at the burrow entrance to be fed. I assumed that parents that returned to the nest, but did not feed nestlings, were unsuccessful foragers (see Brown 1986). I observed 364 cases where parents returned to the nest and remained outside the

TABLE 1. Frequency distribution of departing group size from three Bank Swallow colonies.

Colony size (pairs)	*n* (groups)	Departing group size		
		1	2–4	5–8
26	836	95%	5%	0%
32	449	87%	12%	1%
52	566	86%	14%	0%

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TABLE 2. Frequency distribution of foraging group size at three Bank Swallow colonies.

Colony size (pairs)	*n* (groups)	Foraging group size		
		1	2–4	5–8
26	329	91%	8%	1%
32	51	70%	26%	4%
52	48	94%	6%	0%

burrow, and recorded (a) whether or not they fed the nestlings, and (b) how many birds followed them when they departed from the colony. Successful foragers were followed away from their nest site in 46 of 330 visits (13.3%), while 3 of 34 (8%) unsuccessful foragers were followed ($\chi^2 = 0.57$, df = 1, $P > 0.05$).

If following behavior is a result of information exchange about the location of food resources, then individuals that depart in a group should remain together and feed in the same group. Since the habitat was very open, I was able to observe departing groups until the focal bird began foraging. Birds that were foraging made abrupt turns in pursuit of flying insects, in contrast to the direct flight away from the colony. For all colonies combined, only 15 (19%) of 77 groups of two birds foraged together (within about 50 m of each other). None of 14 groups of three birds remained together, and only one of five departing groups of four birds remained together to feed. Most departing groups separated 30 to 50 m after leaving the colony.

Information transfer about the location of patchy and ephemeral food sources should result in individuals foraging in groups, rather than solitarily. For departing birds observed during the hourly watches, I recorded the size of the group in which it began foraging. Unlike Cliff Swallows (Brown 1988a), foraging groups were not well defined and distinct. To ensure that foraging groups were not overlooked, I defined group size as the number of foraging birds within about 50 m of the focal bird. Foraging groups greater than five individuals were observed in only seven of 48 foraging groups (Table 2). In each colony, most (70 to 94%) departing birds subsequently foraged alone. This contrasts with Cliff Swallow colonies of comparable size, where solitary foragers comprise less than 20% of foraging group sizes (Brown 1988a).

For the 26-pair colony, located in the most open habitat, I also conducted 18 surveys of foraging behavior at different times of day and weather conditions. During each 2-hr survey, at 10-min intervals, I recorded the number of birds foraging in each 45° section around the colony, up to about 300 m away. I never saw large (>20) numbers of Bank Swallows congregating (e.g., on one patch of insects), as described for Cliff Swallows (Brown 1986, 1988a). Foraging birds were usually widely scattered in all directions.

In Cliff Swallows, the degree of information transfer among colony residents increases with colony size (Brown 1988b). The size of Bank Swallow colonies often exceeds 300 pairs (Hoogland and Sherman 1976), so it is possible that information transfer is important in colonies larger than those studied here. However, even in small Cliff Swallow colonies of comparable size (<100 pairs), solitarily feeding birds are unusual, and foraging group sizes of five to 50 birds are commonly observed (Brown 1988a). In a 13-nest Cliff Swallow colony, 71% (233/328) of individuals that departed solitarily circled overhead, and then followed a departing group to a foraging site (Brown 1988b). In the smallest Bank Swallow colony (25 pairs), only 15% (125/836) of departing birds circled at least once above the colony, and these circling birds most often travelled to feeding sites alone.

Although my observations suggest that Bank Swallow colonies do not act as information centers in ways similar to Cliff Swallow colonies of comparable size, observations are needed for large Bank Swallow colonies (>300 pairs). The differences between small Bank Swallow and Cliff Swallow colonies could be due to differences in the distribution of aerial insects in different breeding areas. Social foraging would not be advantageous when food resources are evenly distributed, because local patches of prey would not be large enough to support many foraging birds. Since most Bank Swallows foraged solitarily and were widely scattered in all directions it is possible that food resources used by Bank Swallows in this study area were not patchy and ephemeral. In contrast, in southwestern Nebraska, aerial insects often occur in localized, high density patches, which persist for only 20 to 30 min (Brown 1986).

The absence of information centers in small Bank Swallow colonies may not be universal, since the distribution of prey, and types of prey taken, may vary geographically. Hoogland and Sherman (1976) reported that Bank Swallows from a small colony (five pairs) in Michigan did not depart in groups. Emlen and Demong (1975) stated that Bank Swallows followed each other away from colonies in New York, but they did not indicate how frequently this occurred, whether departing groups remained together to forage, and the colony sizes involved.

Emlen and Demong (1975) proposed that Bank Swallows benefit from group living through social foraging. Although my data are not conclusive, they offer no support for Emlen and Demong's hypothesis. If Bank Swallows do not benefit from social foraging, then why do they nest colonially? As with other Bank Swallow studies (Hoogland and Sherman 1976), there was an abundance of gravel pits and river banks in my study area, suggesting that there was no shortage of suitable nesting habitat. Although there is some evidence that large Bank Swallow colonies are more effective at detecting and subsequently deterring predators than small colonies (Hoogland and Sherman 1976), it is not known whether individuals nesting in large colonies have a lower risk of predation than those nesting in smaller colonies. The major benefits of group living in Bank Swallows remain unknown. The differing importance of information centers as a benefit of group living in Bank Swallows, compared to Cliff Swallows, may represent different selective forces shaping the evolution of group living in these two colonial swallows.

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