

Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators*

CHARLES R. BROWN

Department of Biology, Yale University, P.O. Box 6666, New Haven, CT 06511 U.S.A.

Abstract. Colonially nesting cliff swallows, *Hirundo pyrrhonota*, in southwestern Nebraska, U.S.A., often forage socially, in groups of two to more than 1000 individuals, on ephemeral concentrations of insects. Social foraging was promoted through information transfer among individuals at fixed colony sites, and through local enhancement in which foraging activities of some individuals attracted others to a food source. Cliff swallows feeding in groups had greater average foraging success (prey capture attempts per min) than birds feeding solitarily. Variance in prey capture success, and thus foraging risk, declined with group size and was greatest for solitary foragers. Solitary cliff swallows whose foraging success equalled or exceeded that expected from social foraging remained solitary during a given foraging bout. Solitary foragers whose success fell below that expected from social foraging joined foraging groups. For individuals foraging socially there was no consistent relationship between foraging success and group size, indicating little competition among group members for food and little resource depression. Social foraging in cliff swallows is probably not an adaptation mainly to decrease individuals' risk of predation because foraging success did not differ for birds foraging on the edges versus in the centres of groups, and individuals foraging on the edges did not try to move toward the centre. These data are consistent with risk-sensitive foraging models and provide the first empirical demonstration with free-living animals that social foraging is associated with decreased individual variance in foraging success.

'The Surrounding Plains is open Void of Timber and leavel to a great extent, hence the wind from whatever quarter it may blow, drives with unusial force over the naked Plains and against this hill; the insects of various kinds are thus involuntarily driven to the Mound by the force of wind, or fly to its Leeward Side for Shelter; the small Birds whoes food they are, Consequently resort in great numbers to this place in Surch of them; Perticularly the Small brown Martin of which we saw a vast number hovering on the Leward Side of the hill. . . .'

— Captain William Clark
Spirit Mound, South Dakota, U.S.A.
25 August 1804
(from DeVoto 1953)

Most animals are faced with the choice of foraging solitarily versus socially. The two major advantages of social foraging are (1) enhanced group abilities to locate and/or subdue prey, and (2) enhanced group vigilance against predators. Both of these advantages may lead to increased foraging efficiency by individuals and selection for group feeding in some circumstances (e.g. Pulliam & Caraco 1984). Understanding the nature and derivation of social foraging's potential benefits, and

its potential costs (such as increased competition for food), is essential in evaluating the influence of group feeding on the evolution of animal sociality.

Both breeding and non-breeding individuals forage in groups. Among animals breeding in colonies, social foraging may often be a response to information transfer among individuals and such information transfer may take two major forms (Wittenberger & Hunt 1985). Group members may observe directly where other animals are feeding and use that information to find food themselves, a phenomenon known as 'local enhancement' (Thorpe 1956; Hinde 1961). Alternatively, unsuccessful group members returning to a fixed location (e.g. a colony) may acquire information on the whereabouts and quality of food resources through active or passive signals from returning successful foragers, enabling the unsuccessful individuals to find food by subsequently following the successful animals to the food source. In such situations the breeding colony constitutes an 'information centre' (Ward & Zahavi 1973). Local enhancement and information transfer at a fixed location may occur sequentially or simultaneously for some species, although the phenomena are usually treated separately because foraging via local enhancement does

not require the (Hoogland & Sl
berger & Hunt
monly during ne
benefit of both
that an indivi
increased (e.g. F
Mangel 1984; B

Another imp
whether the fora
or through info
vidual's varianc
foraging risk) m
Clark & Mangel
the best option
above-average co
ance in foraging
that the individu
survival probabi
average conditio
be favoured desp
mizing variance
the individual's
ciently high rat
starvation. Anin
sponse to their e
said to be risk-se

In this paper
swallows, *Hirund*
time on cliff swal
enhancement. C
human vertebrat
mented that colo
(Brown 1986). Th
3000 nests, and
swallow that has
foraging trip re
successful forage
food it brings bac
follows that succe
on its next trip aw
However, this pap
viour of the bird
foraging grounds
and the foraging t
diately upon their
select colonies, w
behaviour during
address the follow
foraging consisten
Is competition for
social foraging? (3

* This paper is based in part on research that received the Animal Behavior Society's W. C. Allee Award in 1984.

not require that the participants nest together (Hoogland & Sherman 1976; Bayer 1982; Wittenberger & Hunt 1985) and may also occur commonly during non-breeding seasons. The presumed benefit of both of these types of social foraging is that an individual's average feeding rate is increased (e.g. Pulliam & Millikan 1982; Clark & Mangel 1984; Brown, in press).

Another important benefit of social foraging, whether the foraging occurs by local enhancement or through information centres, is that an individual's variance in the rate of prey intake (i.e. its foraging risk) may be reduced (e.g. Caraco 1981; Clark & Mangel 1986). Feeding in a group may be the best option for an individual in average to above-average condition, because the reduced variance in foraging success maximizes the likelihood that the individual will maintain its condition and survival probability. For an individual in below-average condition, however, solitary foraging may be favoured despite its greater risk because maximizing variance in the rate of prey intake may be the individual's only hope of achieving a sufficiently high rate of prey encounters to avoid starvation. Animals foraging in this way in response to their expected survival probabilities are said to be risk-sensitive.

In this paper I explore social foraging in cliff swallows, *Hirundo pyrrhonota*, focusing for the first time on cliff swallow foraging that occurs via local enhancement. Cliff swallows are the first non-human vertebrate for which it has been documented that colonies serve as information centres (Brown 1986). These birds live in colonies of up to 3000 nests, and when feeding nestlings a cliff swallow that has been unsuccessful on a recent foraging trip returns to the colony, locates a successful forager, apparently by observing the food it brings back in its throat and bill, and then follows that successful individual to a food source on its next trip away from the colony (Brown 1986). However, this paper addresses the foraging behaviour of the birds once they have arrived on the foraging grounds after travelling from the colony and the foraging behaviour of cliff swallows immediately upon their arrival in the spring before they select colonies, which should reflect their foraging behaviour during the non-breeding season. I address the following questions. (1) Is cliff swallow foraging consistent with risk-sensitive models? (2) Is competition for food a major potential cost of social foraging? (3) Is social foraging a response to

avoiding predators? (4) Has social foraging led to the evolution of coloniality and non-breeding gregariousness in cliff swallows?

STUDY ANIMAL AND STUDY SITES

Cliff swallows are small, migratory passerines that nest in colonies throughout much of western North America. The species nests commonly from the Lower Sonoran through the Transition zones to about 3000 m, but rarely at higher altitudes (Grinnell & Miller 1944). Cliff swallows arrive in the southern and coastal parts of their breeding range in March and arrive in most other areas (including my study area) 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 (American Ornithologists' Union 1983). The birds build gourd-shaped nests out of mud pellets, and the cantaloupe-sized nests are attached underneath overhanging rock ledges on the sides of cliffs and canyons. Relatively recently, cliff swallows in some areas have begun nesting under the eaves of bridges, buildings, highway culverts and other artificial structures that offer an overhanging ledge and a rough vertical substrate for nest attachment. These birds feed exclusively on insects caught in flight, often feeding on dense, ephemeral patches of insects that are concentrated by localized convection currents or by the insects' tendencies to aggregate in mating swarms and mass emergences (Brown 1985). Cliff swallows occur in a wide variety of habitats, although open fields for feeding and a body of water as a mud source are usually located close to each colony. The birds are highly social in all of their activities: feeding, preening, mud-gathering and loafing in large groups (Emlen 1952; Brown 1985). The species is usually single-brooded, and haematophagous ectoparasites are responsible for much of the observed nestling mortality (Brown & Brown 1986). The cliff swallow's general biology has been well studied (Emlen 1941, 1952, 1954; Mayhew 1958; Samuel 1971; Grant & Quay 1977; Withers 1977; Brown 1985).

This study, part of continuing long-term research on the social behaviour of cliff swallows, was done primarily in southwestern Nebraska, U.S.A., near the University of Nebraska's Cedar Point Biological Station, from May to August, 1982-1986. Cliff swallows are abundant in this

area, and have probably increased in recent years with the construction of artificial structures upon which they can nest. These birds occurred in southwestern Nebraska before the appearance of artificial structures, however, nesting on bluffs and outcrops along the North Platte River and also on cliffs in other parts of the state (Nichols, in Pearson 1917). My assistants and I (hereafter, 'we') studied colonies that were located on bridges over irrigation canals, over creeks, and over both the North and South Platte rivers; in culverts under highways; on irrigation structures of various forms; and on natural cliff sites along the south shore of Lake McConaughy. During 1982-1986, we studied 218 cliff swallow colonies totalling 70 545 nests in Keith, Garden and Lincoln counties (Brown 1985). Colony size ranged from 1 to 3000 nests ($\bar{X} \pm \text{SD} = 323.6 \pm 510.0$). The most common colony size was about 350 nests.

Additional observations were made on cliff swallows nesting on the Willis bridge at Lake Texoma, Grayson County, Texas, U.S.A., in March and April, 1982-1983. This colony contained about 350 active nests each year.

METHODS

Observing Foraging Groups

All observations of cliff swallow foraging behaviour were made from vantage points near colonies that provided clear views of the surrounding terrain for a radius of greater than 1 km on virtually all sides. Colonies were located in flat, treeless terrain, facilitating continuous observations of foraging groups and enabling us to follow visually (with binoculars) individual foraging swallows. Observations were usually made on cliff swallows feeding over fields or, more rarely, over lakes. Few observations were made on cliff swallows feeding less than 4 m above the ground, because individuals feeding that low were likely to be obstructed from clear view at times by slight irregularities in topography. Most observations were made on birds feeding 5-15 m above the ground, although cliff swallows at times fed at estimated altitudes of more than 30 m.

Measuring Foraging Success

We observed cliff swallows foraging and counted prey captures per unit time as a measure of foraging

success. These birds show characteristic behaviour when pursuing insect prey. A foraging cliff swallow flies on a level course until it spots an insect and then makes abrupt twists and turns, flying upward (never downward) or to either side to catch the prey item. Once the insect is caught, a swallow rapidly slows, flares its tail noticeably (as an apparent brake), and then returns to nearly its original altitude and resumes flying a level course until another insect is spotted. By observing swallows foraging directly above us and by seeing the birds actually catching insects, we verified that this behaviour does indeed signal prey captures. However, because the insects were sometimes too small for us to see unless swallows were very close to us, we recorded all of this behaviour as prey capture attempts. We are confident that prey capture attempts translated directly to prey captures, because we rarely saw a cliff swallow miss an insect it went after.

We quantified prey capture attempt rates for foraging cliff swallows by recording total observation time with a stopwatch and prey capture attempts with a handcounter. Swallows moving to and from nest or perch sites, or engaged in alarm responses, mud-gathering, or any other non-foraging activities, were not considered for these analyses. Birds were always watched for as long as possible, usually between 45 s and 5 min. An observation was terminated if a bird disappeared from view or if it obviously ceased foraging (e.g. flew to a nest). Prey capture rates were expressed in prey capture attempts per min.

Capture rates were computed for separate 'foraging bouts'. A foraging bout was a period of time on a given day during which weather conditions and birds' foraging altitudes and behaviour were unchanging for the entire time, and during which prey capture rates for different birds were considered comparable. A single foraging bout never lasted longer than 4 h, because temperature, wind and sky cover never remained unchanged for that long. Since the distribution of aerial insects is greatly affected by weather (Johnson 1969), any change in weather could lead to differing prey availabilities and hence to different foraging rates at different time periods. Cliff swallows tended to change their foraging patterns at different times of the day, moving to different altitudes and probably feeding on different prey. For these reasons, statistical comparison of individuals foraging in different bouts was not appropriate. However, between-

bout comparison averages matched-pairs

Scoring Foraging

Cliff swallow groups that all moved. Because efficient operation all the birds within a radius (e.g. continuously) foraging group number of birds observation of group in which forager under to a group of a or departed from that group's site that observation feeding solitary recorded whether ing group while they remained ceased. For birds 15 individuals, individual foraged flock. 'Edge' birds position on the individuals surrounding 'Centre' birds and other foragers continuously. Content in their position virtually all birds either centre or was terminated relative position

For certain group-size class 49, 50-74, and capture attempt individual observed group-size class group's size. The group-size class ate the effect of rate, these groups Spearman rank number of group

bout comparisons were possible by calculating bout averages and comparing these with Wilcoxon matched-pairs signed-rank tests.

Scoring Foraging Group Sizes

Cliff swallows often fed in distinct, well-defined groups that always retained their integrity as they moved. Because groups were so distinct, a sufficient operational definition of a group was usually all the birds within our sight along a given directional radius (e.g. 90°) from our vantage point. We continuously monitored the sizes of surrounding foraging groups, either counting or estimating the number of birds present. Immediately after each observation of an individual forager, the size of the group in which that bird fed was determined. If a forager under observation left its group or changed to a group of a different size, or if other birds joined or departed from the group and thereby changed that group's size by more than approximately 5%, that observation was terminated. Cliff swallows feeding solitarily were also observed, and we recorded whether they subsequently joined a foraging group while they were still foraging, or whether they remained solitary until their foraging activity ceased. For birds foraging in groups of more than 15 individuals, we recorded whether a focal individual foraged on the edge or in the centre of the flock. 'Edge' birds were ones that maintained a position on the group's boundary in which no other individuals surrounded them on at least one side. 'Centre' birds were ones surrounded on all sides by other foragers. Even though they were moving continuously, birds remained remarkably consistent in their positions as they foraged, and thus virtually all birds could be assigned reliably to either centre or edge classifications. An observation was terminated if a focal forager changed its relative position within the flock.

For certain analyses, we established arbitrary group-size classifications of 2-4, 5-14, 15-24, 25-49, 50-74, and 75 or more birds. The mean prey capture attempt rate was calculated for each individual observed, and assigned to the appropriate group-size classification based on its foraging group's size. The mean and variance for each group-size classification was determined. To evaluate the effect of group size on prey capture attempt rate, these group means were analysed with a Spearman rank correlation. Since the maximum number of group-size classifications for each bout

was only six, it was not possible to test (with any effective power) each bout's correlation coefficient for significance.

We recorded the frequency with which foraging groups of different sizes occurred near cliff swallow colonies of different sizes. Although these particular data were collected primarily to investigate spatiotemporal variability in foraging locations and to plot each colony's foraging range (Brown, unpublished data), the resulting information is directly applicable here. These data were recorded by scanning 360° around each colony at 10-min intervals throughout the day or part of the day, noting the size of each group present on the colony's surrounding foraging grounds. Observations were made on up to 14 days from throughout the season at each colony under a variety of weather conditions (but, for the sake of visibility, always when birds fed 4 or more m above the ground). Since individual composition of the groups, positions of the groups, and sizes of the groups were changing frequently, data from each 10-min check were considered statistically independent. The total number of observed foragers from all groups at any given time matched the number of birds in that colony, so we are confident that in each case most of the foragers that we observed were actual colony residents. Colony size was the number of active nests (those containing eggs or nestlings) during the time of these observations on group sizes, and colony size does not include unused nests which occurred commonly in many colonies. See Brown (1985) for further details on how we collected data on group-size frequency and Brown & Brown (1986) for criteria used in separating different groups of cliff swallow nests as different colonies.

Statistical analyses were performed on the Princeton University IBM 3081 computer, using the Statistical Package for the Social Sciences (Nie et al. 1975), and on an IBM XT personal computer, using the PC Statistician (Madigan 1983). All statistical tests were two-tailed. Since most data were not normally distributed, non-parametric statistical tests were used (Siegel 1956).

RESULTS

Foraging by Local Enhancement

The foraging method used most frequently by cliff swallows was to commute from the colony sites

to foraging locations (up to 1 km away) and in the process acquire information at the colony on the success of other returning foragers (see Brown 1985, 1986). Foraging groups formed continually and were maintained by individuals arriving on the foraging grounds from the colony. However, there were other occasions when group foraging developed apparently as a result of local enhancement with no or little information exchange at a colony site. Group foraging of this type fell into three classes.

Network foraging

In network foraging, individuals or groups are loosely spread out over a wide area but within sight of each other (Wittenberger & Hunt 1985). When an individual or a group locates a prey source, other nearby individuals converge on the location. When the food is gone, the foragers disperse again. Network foraging was commonly used by cliff swallows early in the nesting season before the birds began spending much time at the colonies. Foragers spread out over the surrounding fields in either well-defined groups or (more rarely) as solitary birds. Convergence at a particular location by individuals would occur almost instantaneously, with birds apparently observing and cueing on the characteristic prey capture behaviour of the foragers that discovered the insect source. These convergences consisted routinely of 75–1000 cliff swallows that would feed over areas not greater than 10 m². Foragers were sometimes distributed in 'towers' of birds from 0.5 m to more than 30 m above the ground, usually in response to developing swarms of dipterans (principally Chironomidae and Phoridae). Convergences often occurred along streams late in the afternoon, but we also observed them develop on the leeward side of road cuts and bluffs during windy weather (where presumably insects were concentrated) and among trees in canyons during cool and rainy weather. Convergences of cliff swallows at a given site usually lasted 30–45 min, after which the foragers would disperse entirely or re-form at another site 100–500 m away.

More rarely, we observed instances in which an entire foraging group of 50–75 cliff swallows suddenly and in tightly coordinated fashion quickly flew straight to another foraging group up to 100 m away. As soon as they joined the second group, the birds of the first group spread out and began foraging, and the separate groups thereby

merged into a single group. Such instances usually occurred at high altitudes (greater than 30 m) and it was impossible for us to tell if the second group had suddenly found an insect swarm, although that seems likely.

There was no opportunity for cliff swallows to acquire information at a colony site on the foraging locations discovered during network foraging because the birds were not present at the colonies (except for roosting) during the times that network foraging was used most commonly.

Foraging from perches

Another type of local enhancement occurred when cliff swallows assembled in loafing flocks and in creches (Brown 1985), and recruited to food sources nearby. Both early in the nesting season before and during nest building and especially in response to cool, rainy weather, and late in the nesting season after pre-migratory flocking began, cliff swallows assembled in groups of up to 1500 birds that perched on utility wires and in trees. Individuals periodically left these flocks to forage over fields and in canyons nearby, creating continuous arrivals and departures of birds at the flocks. Convergences of foragers at a fixed spot occurred regularly within 75 m of these flocks, during which up to 500 individuals (often many recently fledged juveniles) would leave the flock, fly to the convergence, and feed there for 5–30 min. Individual cliff swallows commuting to and from the flocks discovered these swarms, and their prey capture behaviour appeared to recruit the perched birds that were clearly within visual range. There was no evidence that any sort of information exchange of the sort seen in nesting colonies (Brown 1986) occurred in these perching flocks.

Local enhancement and patch use near colonies

The third foraging situation in which local enhancement was important for cliff swallows occurred when birds exploited relatively long-lasting, patchy concentrations of insects near colonies while feeding nestlings. We were unable to exclude entirely information exchange at the colony site in these situations because foragers commuted from the colony to the foraging sites, but the conspicuousness and closeness to the colony of these foraging convergences suggested that local enhancement was probably very important. Whenever farmers in nearby fields mowed hay, up to 500 cliff swallows converged above and behind the mowers and hawked insects that were flushed by

Table 1. Prey bouts), and compared to

Foraging
A. Solitary Group
B. Solitary joins gr
Solitary does no
Group at same

* Calculat

the machinery. Tractors operating at times, and separate attended each m foraging converg which time cliff s associated with the r occurring within : attracted birds; m m did not attra swallows may hav by following othe relatively long remained active : colony probably by simply flying : them at that mor of birds that trac patterns develop pasture near a ce tall grass, appare ing blood-suckir source for cliff s

Foraging Success

Whether recrui ing individuals concentrations c swallows often numbers of indi day to day. The

Table I. Prey capture attempt rates for (A) cliff swallows that foraged solitarily versus in groups (all bouts), and for (B) solitarily foraging cliff swallows that later joined and did not join groups compared to group foraging birds active at the same time

Foraging action	Prey capture attempts per min per bird per foraging bout				Mean within-bout SD	No. bouts	No. birds observed
	\bar{X} *	SD*	SE*	Range*			
A. Solitary forager	3.6	1.6	0.3	1.3-7.4	2.2	29	504
Group forager	5.9	7.9	1.4	2.2-10.1	2.0	29	1615
B. Solitary forager that joins group	3.4	1.3	0.4	1.8-7.7	3.1	8	70
Solitary forager that does not join group	7.1	2.0	0.7	4.2-10.7	7.8	8	57
Group forager active at same time	6.4	1.8	0.6	4.8-10.1	2.3	8	254

* Calculated on bout means.

the machinery. There were up to three different mowers operating simultaneously in the same field at times, and separate groups of cliff swallows attended each mower. These highly conspicuous foraging convergences lasted for 4-5 h, during which time cliff swallows were continuously associated with the mowers. Only mowing activities occurring within approximately 500 m of a colony attracted birds; mowers operating farther than 500 m did not attract birds. Although some cliff swallows may have initially discovered the mowers by following other individuals from the colony, the relatively long time that these prey sources remained active and their relative nearness to the colony probably enabled birds to use them mainly by simply flying out from the colony and locating them at that moment by observing the large flocks of birds that tracked the mowers. Similar foraging patterns developed when horses were put into a pasture near a colony and began walking through tall grass, apparently stirring up insects and attracting blood-sucking flies (Muscidae), a major prey source for cliff swallows.

Foraging Success of Groups Versus Solitary Birds

Whether recruiting to sources of prey by following individuals from colonies or cueing on dense concentrations of prey via local enhancement, cliff swallows often fed in groups. However, variable numbers of individuals also foraged solitarily from day to day. The first step in evaluating the impor-

tance of social foraging is to examine the relative foraging success of solitary foragers versus that of birds feeding in groups. For this analysis all groups (i.e. two or more birds) were combined regardless of size and only foraging bouts with at least 10 observations of both solitary and group foragers were used. Prey capture attempts per minute were significantly greater for cliff swallows foraging within a group than for birds foraging solitarily ($P < 0.001$, Wilcoxon matched-pairs signed-ranks test; Table IA). This result implies, on average, an advantage to either group foraging per se or to foraging in patches favoured by groups.

To understand why some cliff swallows nevertheless foraged solitarily, we examined (for a subset of the foraging bouts in Table IA) whether solitary foragers remained solitary for the duration of their foraging bout or if they sometimes joined groups, and how these options might be related to a solitary forager's success. These data were collected during eight foraging bouts in which we had a minimum of 15 solitary foragers for whom we knew whether they remained solitary or joined groups. Solitary foragers who remained solitary had significantly higher prey capture attempt rates than did solitary foragers who later joined groups, and also had significantly higher prey capture attempt rates than did birds foraging in groups who were active simultaneously ($P = 0.012$ for each, Wilcoxon matched-pairs signed-ranks test; Table IB). Solitary foragers who joined groups had significantly lower average success while they were solitary than

and a group member's prey capture attempt rate (Table II). Data from these bouts indicated little evidence for resource depression or competition with increasing group size (see also Fig. 1). On eight of 24 (33%) foraging bouts there was a negative correlation between prey capture attempt rates and group size (Table II). Data from these bouts indicated that social foraging at times might lead to resource depression and cause competition among group members. The preponderance of positive correlations (16 of 24) is not significant ($P=0.152$, sign test). There were no seasonal or climatic differences between bouts exhibiting positive versus negative correlation coefficients.

Potential competition with increasing group size might be most likely on days when prey is less abundant, and bouts on these days might result in negative correlation coefficients. We examined whether relationships existed between the sign and the magnitude of the correlation coefficient and the overall mean group foraging success for each of the 24 bouts (Table II). Overall foraging success during bouts with negative correlation coefficients did not differ significantly from foraging success during bouts with positive correlation coefficients (Table II). The magnitude of the correlation also did not vary significantly with overall foraging success for bouts with either positive or negative correlations (Table II). These results suggest that the effects of group size on foraging success are not necessarily related to overall abundance of prey during foraging periods.

A major premise of risk-sensitive foraging models is that group foraging decreases variance in prey encounter rates (e.g. Caraco 1981). We compared variance in mean prey capture attempts per minute for cliff swallows foraging solitary and for individuals foraging in groups of different sizes (Fig. 2). Variance declined markedly with increasing group size (Fig. 2). Reduced variance in larger groups implies that social foraging is less risky to an individual than solitary foraging and that foraging socially in a large group is less risky to an individual than foraging socially in a small group.

Foraging Group Size Frequency and Colony Size

The preceding observations and data indicate that foraging in groups is widespread and advantageous for cliff swallows. During the nesting season whether individuals forage by local enhancement or through information exchange at the

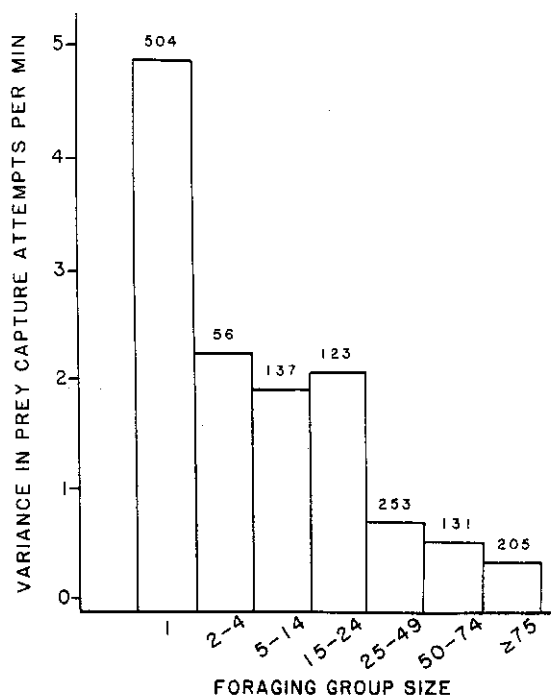


Figure 2. Variance in prey capture attempts per min per bird versus cliff swallow foraging group size. Variances for group sizes of two to 75 or more were calculated by averaging respective variances of each group-size classification for 24 separate foraging bouts in which at least four group-size classifications were represented. These 24 bouts include some bouts that had no solitary foragers and thus that were not used in Table I. For comparison, average variance for solitary foragers from Table I is also shown. Numbers above bars indicate total number of individuals observed for each group-size classification. Variance decreased with group size ($r_s = -0.96$, $P < 0.05$).

colony site, a major determinant of foraging group size and the choice of group size an individual might have is colony size. Larger colonies mean more individuals are potentially present on the colony's foraging grounds at any given time, suggesting that in a large colony a forager might have access to a greater variety of different groups and group sizes than would individuals in small colonies.

For nine cliff swallow colonies, ranging in size from eight to approximately 2000 nests, we examined the percentage of foraging groups of different sizes that occurred on the foraging grounds (Fig. 3). Both average foraging group size and variance in foraging group size increased significantly with colony size (Fig. 3). This means that individuals in large colonies had a greater variety of foraging group sizes and, on average, larger groups to

coefficients for prey swallow foraging s. for 24 separate

Prey empts · bird†	Total no. birds observed
32	32
29	29
33	33
45	45
119	119
60	60
60	60
32	32
65	65
55	55
67	67
48	48
62	62
85	85
68	68
76	76
87	87
124	124
75	75
64	64
106	106
69	69
148	148
41	41

ns for each group- foraging success ns was not signifi- bouts with negative prey U-test). The dent did not vary ess for bouts with negative ($r_s = 0.64$,

availability and g distribution of ferent times and also compared roup size separ- II). For some of ssifications were ip sizes at times s containing at s were included

uts there was a ging group size

individuals that moved from centre to edge comprised 6.9% of the total ($N=1356$). Individuals were thus likely to maintain their relative positions within flocks while foraging.

DISCUSSION

These results indicate that the benefits of social foraging by cliff swallows are at least threefold. Social foraging enhances an individual's ability to locate prey through local enhancement, that is, by observing where others have found prey. Social foraging increases the average prey encounter rate above that expected for solitary foragers. Finally, social foraging reduces variance in prey encounter rate below that expected for solitary foragers. These benefits can result from inherent advantages of social foraging (evolved adaptations) or simply because groups of cliff swallows are actively or passively attracted to higher-quality resource patches, leaving poor-quality patches to solitary foragers (incidental effects). Presently, we cannot distinguish between these two alternatives, and discussion of 'social foraging' in this paper encompasses both possibilities.

Cliff swallows discover insect sources through either local enhancement on the foraging grounds or through information exchange at the colony site (Brown 1986), or through simultaneous use of both. Evaluating the relative frequency and importance of these two foraging strategies during the nesting season is critical, because, of these, only information transfer at a colony favours the evolution of colonial nesting (Bayer 1982; Waltz 1982; Wittenberger & Hunt 1985). Unfortunately, a direct evaluation of this sort for cliff swallows (and perhaps for any species) is difficult. Local enhancement clearly occurred early in the cliff swallow's nesting season and occasionally later in the season, but we had no way to quantify how often cliff swallows discovered prey sources in this fashion. However, the circumstances favouring local enhancement during the nesting season probably occur relatively infrequently. That is, local enhancement occurred most often during the days immediately after cliff swallows arrived in the study area (in Texas, in late March and in Nebraska, in early May), before nest building began, during which time the birds continually foraged together in synchronized flocks (see Emlen 1952). This period typically lasted 5–10 days, a fairly minor

percentage of the cliff swallow's approximately 60-day nesting season in Nebraska. Furthermore, local enhancement was most often associated with unusually dense and abundant swarms of dipterans that remained in a fixed location for up to 30 min or longer, or with disturbances such as mowing and activities of grazing animals near colonies. These situations appeared to occur relatively rarely. Information exchange at the colony site, however, occurred continuously throughout each day during the entire period of nestling feeding (21–24 days), and many incubating individuals also had access to foraging information from neighbours who were already feeding nestlings, effectively increasing the duration of time during which a colony served as an information centre. In addition, the short persistence time and spatiotemporal variability of most cliff swallow prey sources (Brown 1985) suggested that, on average, information transfer at the colony site was a more potentially efficient foraging tactic than local enhancement, since local enhancement generally requires investment of substantial search time between successive discoveries of concentrated but ephemeral prey sources.

Cliff swallows seem to be likely candidates for risk-sensitive foraging, because social foraging is usually more advantageous than solitary foraging, but at times solitary individuals can exceed expected group success (Table I). Diminishing variance in prey encounter rates with group size (Fig. 2) clearly shows that social foraging is less risky to individuals. Although a number of studies (mostly in laboratory settings and on captive animals) have demonstrated empirically that individual foragers usually tend to prefer less risky foraging rewards (e.g. Real 1981; Waddington et al. 1981; Caraco 1982), to my knowledge, there are no previous data that demonstrate the simultaneous occurrence of risk-prone and risk-averse foraging strategies in natural populations of free-living animals. Furthermore, although theoretical models have predicted that social foraging should lead to decreased individual variance in prey encounter rates (e.g. Caraco 1981; Pulliam & Millikan 1982; Clark & Mangel 1984, 1986), these results for cliff swallows (Fig. 2) are apparently the first for any species to support this prediction. As yet, we do not have information on the condition or status of individual cliff swallows who engage in risk-prone solitary foraging, but the results we do have suggest that risk-sensitive foraging models apply to some animals in the wild.

There is little evidence that social foraging regularly leads to competition among members of cliff swallow foraging flocks (Fig. 1, Table II), assuming that such competition would result in lowered feeding rates in the large groups. This lack of evidence is not surprising, given the nature of the cliff swallow's food resource. These birds feed mainly on dense concentrations of dipterans, homopterans and hymenopterans that cluster in mating swarms, emerge en masse, and are concentrated in localized convection currents (Brown 1985). The swarms and emergences are ephemeral and rarely last longer than 10–15 min at any given location. The short duration of, and high density within, these prey 'patches' apparently makes an individual's own harvest so short-lived that there is little cost to sharing the resource with up to hundreds of simultaneously foraging conspecifics. Apparently the foraging activities of increasing numbers of cliff swallows do not regularly lead to either exploitation, microhabitat, or behavioural resource depression (*sensu* Charnov et al. 1976). However, even in cases such as this one where at times enhanced feeding rates in groups lead to presumed benefits of social foraging, competition among group members may still occur in the form of increased foraging effort required to gain an individual's respective share of the available food resource (Clark & Mangel 1986). We were unable to evaluate directly the possible role of foraging effort in social foraging by cliff swallows, and competition of this form might occur in some situations.

The data presented here showing similar foraging success for cliff swallows feeding on the edges versus in the centres of flocks, the relative stability of an individual's position within a foraging group with time, and the lack of aerial predators, indicate that social foraging in cliff swallows is not primarily anti-predator in function. When flying and when away from cover, cliff swallows in Nebraska seemed completely safe from predators. In contrast, when perching in loafing flocks on rock outcrops and in trees or when mud-gathering, these birds were vulnerable to successful attacks by predators, and flocking in these situations appeared to be adaptations to reduce the risk of predation (Brown & Brown 1987). The fact that foraging groups in cliff swallows are probably not anti-predator responses suggests that the benefits of social foraging described here and elsewhere (Brown, *in press*) were responsible for the evolution

of group feeding and that these benefits are not secondary consequences of a behaviour that evolved to reduce predation.

What possible inherent advantages of social foraging in cliff swallows might lead to increased foraging success and decreased variance in prey encounter rates? The possibilities include more efficient search for prey by groups, unintentional or intentional communication among group members about the discovery of prey, and observational learning of prey locations by naive group members from knowledgeable group members (Clark & Mangel 1986). All three factors probably pertain to cliff swallows. Groups, which contain more searchers, are more likely than solitary foragers, on average, to locate the ephemeral and spatially restricted insect concentrations upon which these birds feed. Groups presumably locate insect patches faster than solitary foragers. Although there is as yet little evidence of intentional communication among members of cliff swallow foraging groups about locations of prey, unintentional communication is widespread through both local enhancement and information exchange at the colony site. Both sorts of unintentional communication probably lead to enhanced feeding rates for birds foraging socially. Finally, observational learning of how and on what to forage probably occurs when newly fledged juveniles, while still in creches, forage in groups with adult cliff swallows.

As might be partly expected, cliff swallow colony size affected the frequency of the occurrence of differently sized foraging groups on each colony's foraging grounds. Large colonies, instead of leading to a few huge foraging groups active at any given time, tended to promote the formation of a diversity of foraging group sizes. This means that individuals in large colonies usually had available the apparent option of foraging in small, medium and large groups, or solitarily. To the degree that cliff swallows are risk-sensitive, a major advantage of colonial nesting therefore could be that individuals have simultaneous choices of risk-prone and risk-averse foraging strategies that depend upon individual condition and survival probabilities. Solitarily nesting birds and those nesting in small colonies have limited choice: these individuals are presumably restricted solely to risk-prone solitary foraging or foraging in small foraging groups (where risk is also relatively high: Fig. 2). The occurrence of large foraging groups near large colonies, and thus the higher diversity of

group sizes there search of the fo number of forag more frequent c patches (via eitl colony or local c supporting large risk-averse forag

Social foragin evolution of soc local enhance ment of colonial n group foragin important in the ousness in cliff enhancement us cliff swallows' ar before their dep. foraging behavio activities are no probably reflects the non-breeding gests that cliff sv when on their w tion (Hudson 19 enhanced foragin enhancement and foraging describe benefits of group season. Enhance from informatio primary benefit o (Brown, *in press*) form or another tion of virtually swallows.

ACKN

Many of these da berger Brown. w research. I thank C Karen Brown, R Laura Jackson, I and Todd Scarlett John Janovy, Jr a School of Biologic facilities of the Ce helpful discussion I thank Michael Daniel Rubenstei

benefits are not behaviour that

antages of social lead to increased variance in prey es include more unintentional or g group members and observational e group members mbers (Clark & obably pertain to r contain more litary foragers, on al and spatially upon which these ly locate insect ragers. Although entional commu-swallow foraging y, unintentional rough both local exchange at the tional communi-feeding rates for y. observational orage probably iles, while still in ult cliff swallows. ff swallow colony he occurrence of on each colony's s, instead of lead-ups active at any he formation of a . This means that ally had available o the degree that major advantage ould be that indi-ces of risk-prone gies that depend urvival probabili- l those nesting in oice: these indi-ed solely to risk- ng in small forag- latively high; Fig. ing groups near igher diversity of

group sizes there, may partly reflect more efficient search of the foraging grounds by the increased number of foragers in large colonies. This leads to more frequent discoveries of concentrated insect patches (via either information exchange at the colony or local enhancement) that are capable of supporting large foraging groups and that create risk-averse foraging opportunities.

Social foraging has major implications for the evolution of sociality in cliff swallows. Although local enhancement cannot account for the evolution of colonial nesting, advantages associated with group foraging via local enhancement could be important in the evolution of non-breeding gregariousness in cliff swallows. In Nebraska, local enhancement usually occurs immediately after the cliff swallows' arrival in the spring and immediately before their departure in late summer, and their foraging behaviour during these periods when their activities are not centred at a fixed colony site probably reflects their foraging behaviour during the non-breeding season. Limited evidence suggests that cliff swallows remain highly gregarious when on their wintering range and during migration (Hudson 1951; Hilty & Brown 1986), and enhanced foraging success associated with local enhancement and with the other effects of social foraging described in this paper could be major benefits of group-living during the non-breeding season. Enhanced foraging efficiency resulting from information exchange at colony sites is the primary benefit of colonial nesting in cliff swallows (Brown, in press). Benefits of social foraging of one form or another probably account for the evolution of virtually all spacing behaviour in cliff swallows.

ACKNOWLEDGMENTS

Many of these data were collected by Mary Bomberger Brown, who assisted in all phases of this research. I thank Cathy Boersma, Carol Brashears, Karen Brown, Rachel Budelsky, Laurie Doss, Laura Jackson, Deborah Johnson, Kathi Miller and Todd Scarlett for their assistance in the field. John Janovy, Jr and the University of Nebraska's School of Biological Sciences allowed us to use the facilities of the Cedar Point Biological Station. For helpful discussion or comments on the manuscript, I thank Michael Beecher, John Hoogland and Daniel Rubenstein. Financial support was pro-

vided by the National Science Foundation (a Predoctoral Fellowship and grants BSR-8407329, BSR-8600608), the National Geographic Society, 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, Alpha Chi and Raymond and Kathryn Brown.

REFERENCES

- American Ornithologists' Union. 1983. *Check-list of North American Birds*. 6th edn. Lawrence, Kansas: American Ornithologists' Union.
- Bayer, R. D. 1982. How important are bird colonies as information centers? *Auk*, **99**, 31-40.
- Brown, C. R. 1985. The costs and benefits of coloniality in the cliff swallow. Ph.D. thesis, Princeton University, Princeton, New Jersey.
- Brown, C. R. 1986. Cliff swallow colonies as information centers. *Science, N.Y.*, **234**, 83-85.
- Brown, C. R. In press. Enhanced foraging efficiency through information centers: a benefit of coloniality in cliff swallows. *Ecology*.
- Brown, C. R. & Brown, M. B. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhota*). *Ecology*, **67**, 1206-1218.
- Brown, C. R. & Brown, M. B. 1987. Group-living in cliff swallows as an advantage in avoiding predators. *Behav. Ecol. Sociobiol.*, **21**, 97-107.
- Caraco, T. 1981. Risk-sensitivity and foraging groups. *Ecology*, **62**, 527-531.
- Caraco, T. 1982. Aspects of risk-aversion in foraging white-crowned sparrows. *Anim. Behav.*, **30**, 719-727.
- Caraco, T. & Pulliam, H. R. 1984. Sociality and survivorship in animals exposed to predation. In: *A New Ecology, Novel Approaches to Interactive Systems* (Ed. by P. W. Price, C. N. Slobodchikoff & W. S. Gaud), pp. 279-309. New York: John Wiley.
- Charnov, E. L., Orians, G. H. & Hyatt, K. 1976. Ecological implications of resource depression. *Am. Nat.*, **110**, 247-259.
- Clark, C. W. & Mangel, M. 1984. Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.*, **123**, 626-641.
- Clark, C. W. & Mangel, M. 1986. The evolutionary advantages of group foraging. *Theor. Pop. Biol.*, **30**, 45-75.
- DeVoto, B. (Ed.) 1953. *The Journals of Lewis and Clark*. Boston: Houghton Mifflin.
- Emlen, J. T., Jr. 1941. Cliff swallow colonies of the central Sacramento Valley in 1941. *Condor*, **43**, 248.
- Emlen, J. T., Jr. 1952. Social behavior in nesting cliff swallows. *Condor*, **54**, 177-199.
- Emlen, J. T., Jr. 1954. Territory, nest building, and pair formation in the cliff swallow. *Auk*, **71**, 16-35.
- Grant, G. S. & Quay, T. L. 1977. Breeding biology of cliff swallows in Virginia. *Wilson Bull.*, **89**, 286-290.
- Grinnell, J. & Miller, A. H. 1944. The distribution of the birds of California. *Pacific Coast Avifauna*, **27**, 1-608.

- Hamilton, W. D. 1971. Geometry for the selfish herd. *J. theor. Biol.*, **31**, 295-311.
- Hilty, S. L. & Brown, W. L. 1986. *A Guide to the Birds of Colombia*. Princeton, New Jersey: Princeton University Press.
- Hinde, R. A. 1961. Behaviour. In: *Biology and Comparative Physiology of Birds* (Ed. by A. J. Marshall), pp. 373-412. New York: Academic Press.
- Hoogland, J. L. & Sherman, P. W. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.*, **46**, 33-58.
- Hudson, W. H. 1951. *Letters on the Ornithology of Buenos Ayres*. Ithaca, New York: Cornell University Press.
- Inglis, I. R. & Lazarus, J. 1981. Vigilance and flock size in brent geese: the edge effect. *Z. Tierpsychol.*, **57**, 193-200.
- Jennings, T. & Evans, S. M. 1980. Influence of position in the flock and flock size on vigilance in the starling, *Sturnus vulgaris*. *Anim. Behav.*, **28**, 634-635.
- Johnson, C. G. 1969. *Migration and Dispersal of Insects by Flight*. London: Methuen.
- Madigan, S. 1983. *PC Statistician, the Statistical Report Program*. Northridge, California: Human Systems Dynamics.
- Mayhew, W. W. 1958. The biology of the cliff swallow in California. *Condor*, **60**, 7-37.
- Milinski, M. 1977. Do all members of a swarm suffer the same predation? *Z. Tierpsychol.*, **45**, 373-388.
- Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H. 1975. *Statistical Package for the Social Sciences*. 2nd edn. New York: McGraw-Hill.
- Pearson, T. G. (Ed.) 1917. *Birds of America*. Vol 3. New York: University Society.
- Pulliam, H. R. & Caraco, T. 1984. Living in groups: is there an optimal group size? In: *Behavioral Ecology, an Evolutionary Approach*. 2nd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 122-147. Sunderland, Massachusetts: Sinauer.
- Pulliam, H. R. & Millikan, G. C. 1982. Social organization in the nonreproductive season. In: *Avian Biology*. Vol. 6 (Ed. by D. S. Farner, J. R. King & K. C. Parkes), pp. 169-197. New York: Academic Press.
- Real, L. A. 1981. Uncertainty and pollinator-plant interactions: the foraging behavior of bees and wasps on artificial flowers. *Ecology*, **62**, 20-26.
- Samuel, D. E. 1971. The breeding biology of barn and cliff swallows in West Virginia. *Wilson Bull.*, **83**, 284-301.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.
- Thorpe, W. H. 1956. *Learning and Instinct in Animals*. London: Methuen.
- Waddington, K. D., Allen, T. & Heinrich, B. 1981. Floral preferences of bumblebees (*Bombus edwardsii*) in relation to intermittent versus continuous rewards. *Anim. Behav.*, **29**, 779-784.
- Waltz, E. C. 1982. Resource characteristics and the evolution of information centers. *Am. Nat.*, **119**, 73-90.
- Ward, P. & Zahavi, A. 1973. The importance of certain assemblages of birds as 'information centres' for food-finding. *Ibis*, **115**, 517-534.
- Withers, P. C. 1977. Energetic aspects of reproduction by the cliff swallow. *Auk*, **94**, 718-725.
- Wittenberger, J. F. & Hunt, G. L., Jr. 1985. The adaptive significance of coloniality in birds. In: *Avian Biology*. Vol. 8 (Ed. by D. S. Farner, J. R. King & K. C. Parkes), pp. 1-78. New York: Academic Press.

(Received 22 April 1987; revised 8 August 1987;
MS. number: A4960)