Anim. Behav., 1991, **42**, 551–564

Food-sharing signals among socially foraging cliff swallows

CHARLES R. BROWN, MARY BOMBERGER BROWN & MARTIN L. SHAFFER
Department of Biology, Yale University, P.O. Box 6666, New Haven, CT 06511 U.S.A.

(Received 9 November 1990; initial acceptance 14 December 1990; final acceptance 1 February 1991; MS. number: A5915)

Abstract. Colonially nesting cliff swallows, *Hirundo pyrrhonota*, in southwestern Nebraska use a vocal signal, termed the squeak call, which alerts conspecifics that food has been found. Birds were recruited to playbacks of this call, and the frequency of calling increased when insect swarms were provided to the swallows. Squeak calls were used mostly while birds were foraging in loose groups away from their colonies. Calling occurred primarily on days when temperatures were less than 17°C, solar radiation was less than 500 W/m^2, and wind speed was less than 26 km/h, conditions under which foraging success was presumably poor. Weather conditions appropriate for calling occurred regularly, with an average 24·5% of days in each breeding season suitable for use of the squeak call. Calling probably improves the caller's own foraging efficiency. By recruiting other foragers to a discovered food source, the caller may increase the chances that the insects' movements will be tracked and thus that the caller itself will be able to exploit the insect swarm for a longer time.

Active signals that convey information specifically about food locations and quality occur commonly in social insects (e.g. Wilson 1971), but are largely unknown in vertebrates. More generalized signals that result incidentally in resource sharing are also rare (Smith 1977). Food-sharing signals might be most likely among animals that are brought together at common nest or roost sites, and the few reports of active signalling about food in vertebrates have come from social species. For example, among mammals, Wrangham (1986), Dittus (1984) and D'Vincent et al. (1985) described calls that were given when food was discovered in groups of chimpanzees, *Pan troglodytes*, toque macaques, *Macaca sinica*, and humpback whales, *Megaptera novaeangliae*, respectively. Among birds, Elgar (1986) and Heinrich (1988) reported that flocking house sparrows, *Passer domesticus*, and ravens, *Corvus corax*, respectively, used calls in winter that attracted conspecifics to food sources, and Evans (1982) and Evans & Welham (1985) found that gulls, *Larus* spp., leaving a colony called apparently to recruit conspecifics to follow them, perhaps to food. Greene (1987) described a rarely used visual display by ospreys, *Pandion haliaetus*, returning to their nests that may have informed other individuals of the foraging success of the returning bird. However, other than anecdotal observations on a possible food-finding signal in cliff swallows, *Hirundo pyrrhonota* (Stoddard 1988), there have been no reports of colonial birds using specific food calls to inform one another of the location of food. We have discovered a previously unknown vocalization in cliff swallows that may be used exclusively to signal the discovery of food and results in the sharing of food with conspecifics that are probably often unrelated to the caller.

Cliff swallows breed in colonies that serve as information centres (Brown 1986). Until now, all information transfer in this species was believed to be unintentional or passive, with individuals simply observing others and following successful birds to ephemeral patches of insect prey (Brown 1986). Active communication about locations of food potentially augments any advantages associated with information centres (Ward & Zahavi 1973; Brown 1988a). Moreover, the apparently intentional sharing of information with conspecifics that may be unrelated poses potential problems with the accepted view that animals should act in their own interests and generally avoid aiding potential genetic competitors (e.g. Williams 1966; Dawkins 1976; Heinrich 1988). In this paper we describe food-sharing signals in cliff swallows and the ecological contexts in which they are used, and speculate on the evolution of these signals.

0003–3472/91/100551+14 $03.00/0 © 1991 The Association for the Study of Animal Behaviour

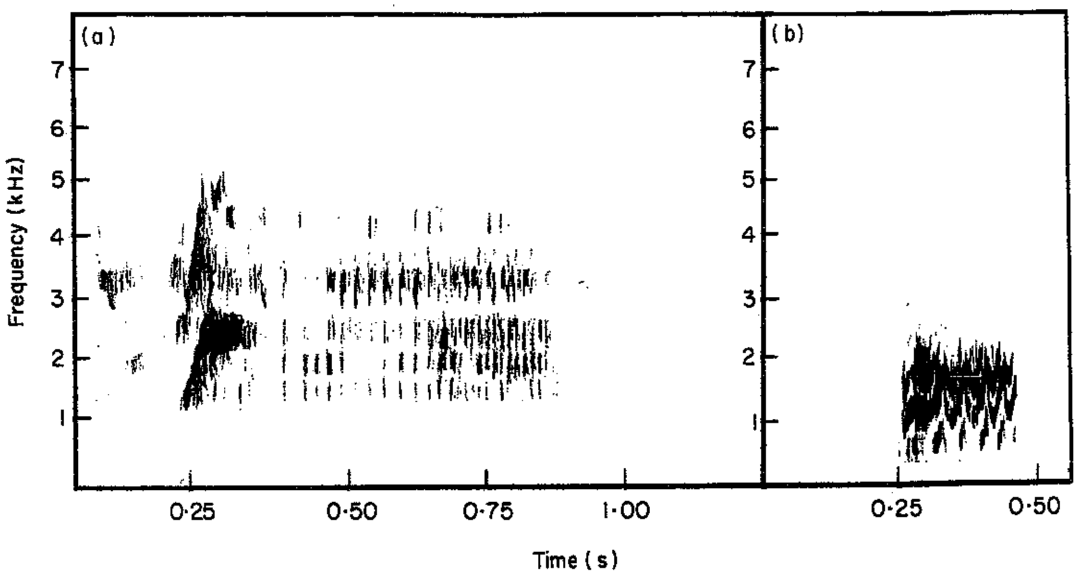

Figure 1. Sonagram of a typical cliff swallow squeak call (a) and a typical chur call (b).

METHODS

Study Animal and Study Site

Cliff swallows are small migratory passerines that nest in colonies throughout much of western North America. They arrive in the southern and coastal parts of their breeding range in March and arrive in most other areas (including our study area) by early May. Most cliff swallows leave North America in August and September for their wintering range in South America. The birds build gourd-shaped nests out of mud pellets, and their nests are attached underneath overhanging rock ledges on the sides of steep cliffs or on artificial structures such as bridges. Cliff swallows feed exclusively on insects caught in flight, often on swarms created by insect mating flights or mass emergences (Brown 1985a). Cliff swallows are highly social in all of their activities; they feed, preen, gather mud and migrate in large groups.

Our study was conducted in southwestern Nebraska near the University of Nebraska's Cedar Point Biological Station, in 1982–1990. Cliff swallows are abundant in this area, and have probably increased in recent years with the construction of highway culverts and bridges upon which they can nest. These birds also occurred in southwestern Nebraska before the appearance of artificial structures, nesting on bluffs and outcrops along the North Platte River and on cliffs in other parts of the state (Nichols, cited in Pearson 1917). Colonies in our study area were situated on bridges, in highway culverts, on irrigation structures and on natural cliff sites along the south shore of Lake McConaughy. Mean ($\pm$SE) colony size in Keith, Garden and Lincoln counties was 381 ± 31 nests ($N=401$ colonies; range 2–3700 nests). Some cliff swallows also nested solitarily.

Rationale for Experiments

The call we identified as a probable food-finding signal was the squeak call (Fig. 1a). We conducted playback experiments using the squeak call to determine to what degree the squeak call itself recruited foraging cliff swallows. If the call attracted foragers, there should have been an increase in foraging swallows during the time the call was broadcast, relative to the number of birds present before the playback. No food was provided to the birds during these playbacks.

We also broadcast another cliff swallow vocalization as a control, using the same protocol and under the same weather conditions as those under which we presented the squeak call. We chose the chur call as our control (Fig. 1b), a seemingly general-purpose signal used in virtually all contexts both at and away from the colonies (Brown 1985b). The chur call, an alarm call, and the male's song are the only three vocalizations commonly used by adult cliff swallows.

We examined tendencies of cliff swallows that were not actively foraging to respond to squeak calls near the colony sites. We broadcast the calls at distances of 25 and 100 m from the colonies. The 25-m distance tested whether birds at the colony would respond; 25 m was as close as we could get and still be able to resolve potential responses to the playback from normal flights into and out of the colony. The 100-m distance tested whether birds that were primarily commuting to and from the colony and foraging sites would respond. We conducted experiments at five colonies of different sizes to see if colony size might affect the birds' tendencies to respond.

If the squeak call signals the presence of food and thereby causes recruitment, the incidence of calling should increase when a food source is provided to these birds. The alternative could be that squeak calls are given by birds that group together for reasons unrelated to the presence of food.

The only way to provision cliff swallows with food artificially was to flush insects out of grass, akin to the movements of large grazing animals or mowing activities that stir up insects, to which these birds quickly recruit (Brown 1988b). Chironomids (Diptera: Chironomidae) occurred in vast numbers in the Cedar Point Biological Station area, and birds foraging over grassy fields in this area probably fed almost exclusively on chironomids during the cool and cloudy weather during which squeak calls were used. These insects rested in the grass during cool and cloudy weather; in warm weather they apparently dispersed and/or flew higher. Our flushing activities caused the chironomids to rise out of the grass up to 2 m above the ground and maintain dense swarms for 1–2 min before dispersing, either by settling back in the grass or being blown by wind currents. Few insects appeared to be flying before we flushed them, meaning that our provisioning probably resulted in a major, though quite temporary, increase in available food for the foraging birds.

Playbacks and Recordings

For the playbacks at foraging sites, we conducted all experiments in a grassy field at the Cedar Point Biological Station. We broadcast the playback in the centre of a rectangular area measuring 25·6 × 30·6 m (783 m^2) and delineated on all sides by rows of low (< 3 m high) eastern red cedar trees, *Juniperus virginiana*. We could hear the playback tape easily from all parts of this rectangular area, and the area was small enough to allow us to see all birds entering it. The operator of the tape recorder sat in the centre of the playback area, and another person, who counted all birds present, was positioned on the top of a small bluff about 50 m to the east and about 15 m above the playback area. This vantage point allowed the observer to see and count all cliff swallows that passed through the playback area easily, because the birds usually fed quite low to the ground (⩽3 m) during the experimental periods. Any cliff swallow that passed over any part of the defined playback area during the designated observation period was counted. Although some double counting of birds was unavoidable whenever an individual left the playback area and returned during the same observation period, our impression was that birds seldom did this, and any double counting effect was presumably constant across all observation periods. Foraging swallows seemed to ignore completely the presence of both the observer and the operator of the tape recorder, often passing within 1 m of both.

For playback experiments at the colonies, we used colony sites of 10, 140, 500, 1000 and 1100 active nests. We broadcast the playback from a tape recorder mounted on the roof of a car, and the observer sat inside the car (which had a sunroof that was opened fully to allow us to see all birds directly overhead). We counted all cliff swallows that passed within 10 m to the sides, front, or above the car during an observation period. This was a smaller overall playback area than that used at the foraging sites, but a smaller area was necessary to achieve manageable counts of birds because of the large numbers of birds flying into and out of some of the colonies. Each of these colonies was situated in a highway culvert, which allowed us to approach on either side along the road. We conducted a separate series of playbacks at distances of 25 and 100 m from each culvert. We alternated approaching from either side of the colony for each distance. We did all playbacks at colonies on 1–18 July 1987, when virtually all active nests in each colony contained nestlings.

All playback experiments consisted of counting the total number of birds present in the designated area for three 2-min periods: one before the playback, one during the playback and one after the playback. For a given set, there were no breaks between the three observation periods. After each set, we waited at least 5 min, and sometimes up to 20 min, before beginning another set. To minimize the likelihood of the birds habituating to the playback at the colonies, we performed only one set of observations at each distance each day, requiring visits to each colony on 10 different days. Weather conditions suitable for playbacks at the foraging sites occurred less often, however, and therefore for those playbacks we conducted multiple sets on the same day. To minimize the potential for habituation at that site, we conducted no more than 10 sets during any single 4-h period or on any given day. On 3 days suitable conditions for playbacks persisted throughout the day, and in these cases we performed a series of playbacks in both the morning and the afternoon. We judged this acceptable because there were large numbers of cliff swallows present at the foraging sites on these days, and we probably broadcast to different individuals at different times. We counted birds in the playback areas with hand-counters. If less than five birds were present in the playback area before playback, we terminated the experiment for that day, because that suggested that there were probably few if any birds available to hear the broadcast calls. An exception to this was made for playbacks performed at the 10-nest colony, where the small number of birds available made the five-bird criterion unrealistic; at this site, we conducted experiments regardless of the number of birds present before playback.

We broadcast playbacks on a Nagra III tape recorder (using the recorder's speaker) at maximum volume (15 dB). This volume provided minimal distortion. For both squeak and chur calls, playback tapes broadcast approximately 38 calls/min. Calls from at least five different individuals recorded at different sites were represented on each playback tape and presented in alternating order, a recommended design in playback studies (Kroodsma 1989). We made field recordings of calls with a Dan Gibson Electronic Parabolic Microphone and Nagra III tape recorder. We recorded most examples of the squeak call on 22–23 May 1987 at foraging sites near the Cedar Point Biological Station when hundreds of foraging cliff swallows were present. We recorded examples of the chur call at colony sites on 18–28 July 1989. Sonagrams (Fig. 1) were made on a Kay Elemetrics Sona-Graph Model 6061-B using wide band pass setting and linear scale.

For statistical analysis of the results of the playback experiment, we used non-parametric Wilcoxon matched-pairs signed-rank tests (Siegel 1956). This allowed us to compare results between experiments performed on the same day, or between averages for experiments performed on different days. Matched-pairs tests were appropriate because each set of experiments was done under slightly different conditions that varied because of weather, date, and most importantly, the number of birds present in the area immediately before the experiment.

Food Provisioning

A strip of grassy field measuring 60 × 30 m (1800 m^2) near the Cedar Point Biological Station was selected as a provisioning plot. The plot was bordered on the long sides by two parallel dirt roads and set off on the two ends by telephone poles. Swarms of chironomids were flushed simply by walking briskly from one end of the plot to the other, hitting the tops of the grass with a 1-m stick using a side-to-side motion. It took about 1·5 min to walk through the plot. Upon reaching the end of the plot, the observer moved to the dirt road, thus stopping any further flushing. The provisioning experiments consisted of counting all birds passing through the plot at any altitude and the total number of squeak calls heard for 2 min immediately before flushing and 2 min immediately after flushing. The observer counted birds and calls while standing on one of the dirt roads near the middle of the plot, which afforded excellent visibility. As with playback experiments, some double counting of birds moving into and out of the plot probably occurred, although its effect was presumably constant across observation periods. We waited at least 10 min between the end of one set of observations and the start of the next; this time appeared sufficient for all insects flushed on the previous trial and all congregated birds to disappear completely. The maximum number of experiments (sets) done consecutively on a single day (with one exception) was 11; it appeared that repeated flushing over longer periods sometimes temporarily depleted the chironomids in the plot. On one day when appropriate weather conditions persisted throughout the day, we did a separate series of food provisioning experiments in the morning and the afternoon. In this case a 2-h interval of undisturbed time between the last morning experiment and the first afternoon experiment seemed sufficient for the insects to reappear in the plot in large numbers.

As with the playback experiments, results of provisioning experiments were analysed with non-parametric Wilcoxon matched-pairs signed-rank tests.

Weather Data

Weather data were recorded in 1985–1987 at a weather station situated at Kingsley Dam, Keith

County, Nebraska, within the study area. This station was about 2 km from the Cedar Point Biological Station where we studied cliff swallow foraging and 5–15 km from the colony sites we studied. In the remaining years, when the Kingsley station was not in operation, weather data were taken from a station (the closest available) at Arthur, in Arthur County, about 40 km directly north of the study area. Once each hour these stations recorded instantaneous temperature, solar radiation, wind speed and direction, and cumulative rainfall within the hour. Data were transmitted upon collection to the University of Nebraska's Department of Agricultural Meteorology in Lincoln, where they were stored on computer. Hourly data on temperature, solar radiation and wind were matched to the times of day when playbacks, provisionings or observations were conducted. The closest hourly reading to a given event was considered to represent the weather conditions under which that event occurred.

We characterized the weather conditions under which squeak calls were used and not used. We identified a total of 36 days during the study when we observed cliff swallows giving squeak calls and another 36 days from the same months on which we did not hear squeak calls, or observe cliff swallows foraging in places or ways in which these calls were used. We randomly selected the 36 'non-calling' days from a larger pool of days when squeak calls were apparently not used. For the non-calling days we used the same times of day that squeak calls were known to have been used. We matched these hours for both calling and non-calling days to the appropriate hourly weather conditions.

RESULTS

Natural Contexts of Calling

We identified one cliff swallow vocalization that was associated exclusively with recruitment to food sources, the squeak call (Fig. 1a). This call appeared structurally similar to portions of the male's courtship song described by Brown (1985b), although to our ears the squeak call was distinct and did not sound like a courtship song. The call was always heard from birds in flight.

The squeak call was given only by swallows that were actively foraging away from their colonies. During hundreds of hours spent at colonies in 9 years of research on this population, we never heard squeak calls by birds either at their nests or flying within sight of a colony. Squeak calls were most commonly heard from birds that were 'network' foraging (sensu Wittenberger & Hunt 1985), that is, spread out in loose flocks over relatively wide areas. Calls obviously attracted other foragers, often with marked convergences of birds into a relatively dense and well defined foraging group. Such groups generally remained together at a relatively fixed site for several minutes, and then either drifted away mostly intact or broke up entirely. Squeak calls were given by birds foraging from 1 to at least 30 m above the ground, but were usually heard from cliff swallows feeding at low altitudes, from 1 to 4 m. We may have underestimated the extent of calling by birds foraging at high altitudes, however, because of the difficulty in seeing or hearing birds there. Cliff swallows routinely feed at 25–30 m, generally in warm and sunny weather when thermals of rising air concentrate insects in patches (Brown & Brown, personal observation).

Squeak calls were often given by cliff swallows foraging over grassy fields and cedar-clad bluffs near the Cedar Point Biological Station. Foraging flocks at this site consisted of probable migrant birds in early spring (late April to May) as well as residents from nearby colonies. On certain days, up to 5000 cliff swallows were estimated to be foraging within 1 km of the biological station, often over a nearby lake. We never heard squeak calls given by swallows foraging over water, although one of us (M.L.S.) made repeated attempts to hear and record squeak calls from over-water foragers.

Another, less frequent context in which squeak calls were given occurred when virtually all cliff swallows were foraging low (< 1 m) over the surface of Lake Keystone and an adjacent canal in the study area. In cold weather (< 10°C), birds resorted to foraging almost exclusively over water, mostly picking insects directly off the surface. In these instances solitary birds would at times leave the lake, fly over the nearby fields and bluffs, and shortly return to the lake. Squeak calls were sometimes given as these individuals, while still flying high above the shore, returned to resume foraging over the water. We saw no indication that the squeak call in these contexts resulted in recruitment towards the caller.

Squeak calls were given only on days that were relatively cool, cloudy and, to some extent, rainy, environmental conditions that are presumably harsh for swallow foraging (Fig. 2). Temperatures during squeak-calling were 17°C or less on 95% of

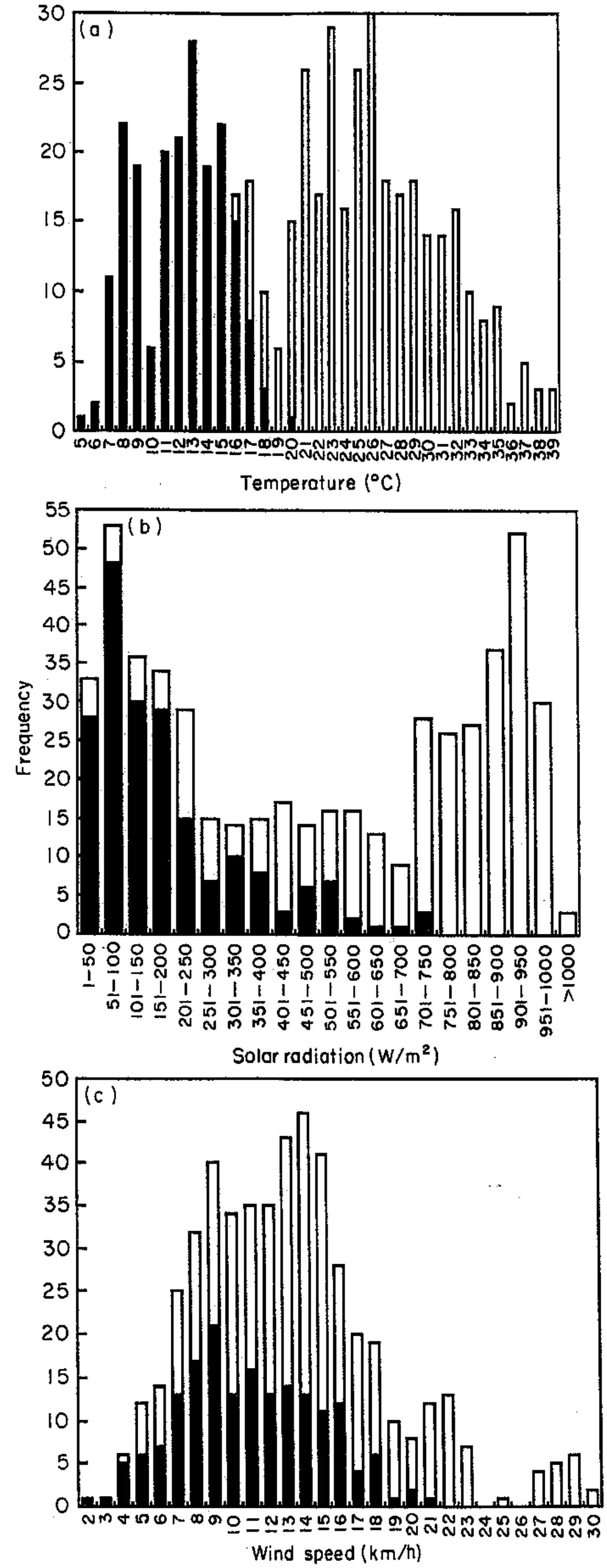

Figure 2. Frequency distributions of temperature (a), solar radiation (b) and wind speed (c) readings taken hourly during times when cliff swallows were known to give squeak calls (■) and during times when squeak calls were never heard (□). For comparison, the mean daily high temperature for May–July recorded at Arthur over a 30-year period was 26·4°C (from Wilhite & Hubbard 1989) and completely clear skies at mid-day would register 800–1000 W/m^2.

Table I. Numbers of cliff swallows counted in 2-min periods before, during and after playback of squeak calls in a field where the birds foraged, for 16 experimental periods*

Period	Mean (±SE) no. of birds			No. of playbacks (N)
	Before	During	After	
19 May 1988	39·4± 6·6[a]	121·4±28·8[b]	78·1±20·6[c]	10
2 July 1988 a.m.	10·7± 1·9[a]	19·7± 3·7[b]	18·7± 7·9[a,b]	7
2 July 1988 p.m.	67·0±21·9[a]	104·5±27·7[b]	74·5±25·5[a]	6
30 May 1989 a.m.	106·7±25·7[a]	134·6±32·5[b]	131·7±36·8[a,b]	9
30 May 1989 p.m.	260·1±18·3[a]	334·8±19·8[b]	281·1±18·4[a]	10
31 May 1989	39·3± 4·0[a]	48·1± 5·6[a]	68·6±11·8[b]	10
9 June 1989	60·8± 8·6[a]	94·1±11·3[b]	58·3± 7·7[a]	10
10 June 1989	5	18	16	1
23 June 1989	21·0± 2·6[a]	38·5± 4·1[b]	20·0± 3·5[a]	6
25 June 1989	22·8± 3·2[a]	32·3± 4·8[a]	22·1± 3·3[a]	6
24 May 1990 a.m.	21·2± 6·8	41·5± 8·7	18·3± 4·2	4
24 May 1990 p.m.	14·8± 4·0	30·0± 4·8	13·8± 9·6	5
29 May 1990	8·8± 3·6	20·8± 5·8	21·5±11·4	4
14 June 1990	16·3± 5·6[a]	35·5± 7·0[b]	19·3± 6·2[a]	6
15 June 1990	11·7± 4·6[a]	23·8± 3·5[b]	12·2± 5·5[a,b]	6
16 June 1990	12	42	12	1

*For each row (where $N \geqslant 6$) mean values not sharing superscript letters differed significantly ($P<0·05$, Wilcoxon matched-pairs signed-rank tests).

the occasions and 15°C or less on 90% (Fig. 2a), and calling did not occur at all when temperatures were over 20°C. Solar radiation scores of 500 W/m^2 or less occurred on 93% of occasions (Fig. 2b), meaning conditions during calling were almost always cloudy. Squeak calls were seldom used in extremely windy weather; calling occurred when wind speed was 26 km/h (16 m/h) or less on 94% of occasions (Fig. 2c).

Playbacks at Foraging Sites

Playbacks in the grassy field where cliff swallows foraged indicated marked recruitment to the squeak call (Table I). There were 11 days or half-days in which we performed at least six separate sets of playbacks (six being the minimum for meaningful statistical analysis; Siegel 1956). On 9 of those days, significantly more birds were present during the playback than before (Table I), and on one of the remaining days (25 June 1989) the difference approached significance ($P=0·071$). When daily means for all 16 playback-days were considered (Table I), there was a significant increase in birds during the playback relative to before ($P<0·001$). The responses to the playback were at times dramatic, with large numbers of birds swirling and circling above the tape recorder. Individual swallows passing through the playback plot in straight-line flights would swerve towards the tape recorder as soon as the broadcast began, circle overhead and usually within 30–60 s, fly out of the plot.

Recruitment to the call did not last long; in most cases, birds had departed and the number present in the plot declined in the 2 min after the playback (although, on average, there were still more birds present after the playback than before: Table I). On only two of 11 individual days was the number of birds present after playback significantly greater than the number present before (Table I), although when daily means for all 16 days were considered, more birds were present after than before ($P=0·022$). There were significantly more birds present during the playback than after on seven of 11 individual days (Table I) and when all 16 daily means were considered ($P=0·004$). The quick decline in numbers of cliff swallows present when playback was stopped probably occurred because there were no developing insect swarms accompanying our broadcast of squeak calls.

Cliff swallows could have responded merely to noise associated with the playback rather than to the squeak call per se. However, birds foraging in the

Table II. Numbers of cliff swallows counted in 2-min periods before, during and after playback of chur calls in a field where the birds foraged, for six experimental periods*

Period	Mean (±SE) no. of birds			No. of playbacks (N)
	Before	During	After	
24 May 1990 a.m.	40·2±2·6	43·0±7·9	39·3± 3·3	4
24 May 1990 p.m.	24·0±8·0^{a}	22·2±8·4^{a}	22·8± 9·5^{a}	6
29 May 1990	25·2±8·9^{a}	14·3±5·5^{b}	23·0±16·2^{a,b}	6
14 June 1990	22·2±6·8^{a}	16·0±6·2^{a}	14·5± 4·3^{a}	6
15 June 1990	18·2±3·5^{a}	22·3±4·1^{a}	28·5± 9·4^{a}	8
16 June 1990	29·0±3·0	24·5±2·5	27·0± 4·0	2

*For each row (where $N \geqslant 6$) mean values not sharing superscript letters differed significantly ($P<0·05$, Wilcoxon matched-pairs signed-rank tests).

Table III. Numbers of cliff swallows counted in 2-min periods before, during and after playback of squeak calls at distances of 25 and 100 m from colonies of different sizes*

Colony size	Distance (m)	Mean (±SE) no. of birds		
		Before	During	After
10	25	1·4± 0·5^{a}	1·2± 0·4^{a}	1·1± 0·4^{a}
10	100	1·2± 0·3^{a}	1·1± 0·4^{a}	1·4± 0·6^{a}
140	25	24·3± 4·4^{a}	30·7± 4·9^{a}	31·1± 4·3^{a}
140	100	8·2± 1·9^{a}	7·2± 1·3^{a}	7·1± 1·6^{a}
500	25	35·1± 5·3^{a}	41·4± 6·3^{a}	39·7± 5·6^{a}
500	100	10·9± 2·2^{a}	15·3± 3·1^{b}	12·1± 2·9^{a,b}
1000	25	75·9±10·7^{a}	87·9±12·1^{b}	90·9±11·7^{a,b}
1000	100	16·0± 5·2^{a}	24·3± 6·8^{a}	18·9± 5·4^{a}
1100	25	55·0± 9·8^{a}	63·6±15·9^{a}	53·5±11·9^{a}
1100	100	7·2± 2·0^{a}	13·5± 3·2^{a}	8·6± 1·8^{a}

*For each row mean values not sharing superscript letters differed significantly ($P<0·05$, Wilcoxon matched-pairs signed-rank tests, $N=10$ each row).

grassy field ignored playbacks of the general-purpose chur calls. There was no significant increase in birds present during the playback of the chur call relative to before the playback on any day (Table II). The only significant difference was on 29 May 1990 when there was a significant decrease in birds during the chur call playback ($P=0·044$), a result not seen with squeak call playbacks. When daily means for all 6 days or half-days with chur call playbacks were considered (Table II), there were no significant differences in number of birds present between any of the observation periods ($P>0·05$). Thus, cliff swallows responded to the squeak call itself and apparently not to more generalized vocalizations or tape-recorder noise in these situations.

Playbacks at Colonies

The fact that we did not hear squeak calls at the colony sites suggested that this signal may be specific to foraging birds. With the exception of the 10-nest colony, where there was no evidence of any response, squeak-call playbacks tended to cause slight recruitment at both 25 and 100 m (Table III). Most of these differences were not significant, however. The only significant differences between

Table IV. Numbers of cliff swallows counted and numbers of squeak calls heard in 2-min periods before and after insects were flushed, for eight experimental periods*

Period	Mean (±SE) no. of birds		Mean (±SE) no. of calls/bird/2-min		No. of trials (*N*)
	Before	After	Before	After	
8 May 1990	37·8± 5·6	240·3±31·3	0·062±0·017	0·267±0·033	11
9 May 1990	9·5± 2·3	20·5± 4·6	0·000±0	0·137±0·014	4
24 May 1990 a.m.	9·7± 2·8	22·7± 5·6	0·000±0	0·100±0·037	6
24 May 1990 p.m.	30·8±10·5	88·7±23·4	0·053±0·025	0·171±0·049	9
27 May 1990	7·9± 3·1	45·4±11·7	0·031±0·020	0·133±0·023	7
29 May 1990	8·8± 5·2	54·8±17·8	0·000±0	0·098±0·014	5
30 May 1990	8·5± 6·5	38·5±28·5	0·033±0·033	0·109±0·009	2
15 June 1990	25·9± 4·0	102·1±15·1	0·032±0·020	0·134±0·025	7

*For each period there were significantly more birds counted after flushing than before and significantly more calls heard after flushing than before ($P<0·05$, Wilcoxon matched-pairs signed-rank tests).

observation periods occurred at 25 m in the 1000-nest colony and 100 m in the 500-nest colony, in which cases significantly more birds were present during the playback than before (Table III).

Most of the playbacks of the squeak call near the colonies, however, occurred when weather conditions presumably were less harsh than the conditions during the foraging-site playbacks. This was simply because early in the season birds deserted their colonies whenever the weather became severe and congregated on foraging grounds, and because harsh weather seldom occurred later in the season when birds remained at their colonies to brood and feed nestlings regardless of the weather. The 100 playback sets we did near colonies (Table III) were matched to their respective weather conditions; of 96 hourly temperature readings taken during the times playbacks were done at colonies, 85·4% were greater than 17°C. Similarly, 48·9% of solar radiation readings taken during playbacks at colonies ($N=94$) were greater than 500 W/m^2. Most of the playbacks at colonies (Table III), therefore, were conducted during warm and relatively sunny conditions.

Only 13 of 100 squeak-call playback sets performed near colonies could be conducted under the same weather conditions as the playbacks at foraging sites (temperature ≤17°C, solar radiation ≤500 W/m^2, and wind speed ≤26 km/h). We pooled those 13 and disregarded distance and colony size. For those playbacks, the results ($\bar{X}$±SE) were 22·1±7·2 birds counted before the playback, 32·3±9·7 birds during the playback, and 23·7±8·3 birds after the playback. These results matched those obtained from playbacks on the foraging grounds, with significantly more birds present during the playback than before ($P=0·020$) or after ($P=0·014$), but no difference between the before and after periods ($P=0·470$, $N=13$ on all, Wilcoxon matched-pairs signed-rank tests). Thus, weather conditions seemed to have a strong effect on whether birds near colonies recruited to the squeak-call playback. (We could not conduct complementary playbacks at foraging sites during warm and sunny conditions because, at those times, cliff swallows fed so high above the ground that they would probably have been unable to hear playbacks from tape recorders on the ground. The birds also ranged further and were less concentrated in potential playback sites during warm and sunny weather.)

Food Provisioning

The number of cliff swallows present and the number of squeak calls heard both increased markedly after food was provided (Table IV). The increase in the number of birds foraging on the flushed insects was statistically significant (Table IV) and not surprising, although their rapid response was unexpected and was perhaps facilitated by squeak calls. The incidence of squeak-calling per bird was significantly greater after food was provided than before (Table IV). On 3 of the 8 days we heard no squeak calls before provisioning on any of the trials but relatively large numbers of calls after

(Table IV). No chur calls or any other cliff swallow vocalizations were heard either before or after provisioning on any of the trials.

Effects of Weather

Since weather seemed to influence whether the squeak call was used and whether birds responded to it, we examined weather patterns associated with recruitment to playbacks (Table I) and calling in response to food (Table IV). Perhaps weather could account for the differences between days in observed recruitment and calling patterns, and might affect calling behaviour by directly affecting the aerial insect prey itself.

For the food provisioning experiments, the mean percentage increase in calls per bird after provisioning relative to before, on a given day, was inversely related to mean wind speed during the trials ($r_S = -0{\cdot}857$, $N=8$, $P=0{\cdot}007$). This meant that cliff swallows showed a greater increase in their rate of calling when food was provided on calm days than on more windy days. For example, on 3 days with average wind speeds less than 13 km/h, the average percentage increase in calling was 326%, whereas on 3 days with wind speeds greater than 22 km/h, the average percentage increase in calling was only 112%. There was no significant effect of either temperature ($r_S = -0{\cdot}191$, $P=0{\cdot}64$) or solar radiation ($r_S=0{\cdot}167$, $P=0{\cdot}66$) on the percentage increase in calling in response to food.

For the playback experiments on the foraging grounds ($N=14$), there was no significant effect of either mean temperature ($r_S=0{\cdot}385$, $P=0{\cdot}17$), solar radiation ($r_S=-0{\cdot}160$, $P=0{\cdot}59$), or wind speed ($r_S=0{\cdot}337$, $P=0{\cdot}24$) on the mean percentage increase of birds recruited during playback on a given day.

Frequency of Conditions for Squeak-calling

Because the use of squeak calls appeared to be restricted to certain types of weather conditions, we examined how often these sorts of conditions occurred. We designated weather conditions in which the temperature was $\leqslant 17°C$, solar radiation was $\leqslant 500\ W/m^2$, and wind speed was $\leqslant 26$ km/h, as conditions in which squeak calls were likely to be used (Fig. 2). All three variables had to meet these criteria simultaneously. Hourly weather data for each day were examined, and any hourly reading in which all criteria were met was considered to represent a suitable hour for squeak-calling. Any day with at least two such hours was considered to be a day suitable for squeak-calling. These weather conditions frequently occurred before 0700 hours, but we only used weather data between 0700 and 1900 hours (the latter time being when most cliff swallow foraging for the day had stopped). These arbitrary criteria for designating a day as suitable for squeak calls were conservative and probably caused us to underestimate the true extent of suitable conditions, especially because squeak calls were occasionally given on warmer and sunnier days (Fig. 2).

For each year from 1982 to 1990, we examined weather data for all days (total 63 days/year) from 1 May to 2 July. Relatively few cliff swallows have arrived in the study area prior to 1 May and 2 July was the latest date in the season on which we heard a squeak call given (although some cliff swallows remain in the study area until mid-August). On average, 24·5% of days each breeding season had weather conditions suitable for squeak calls, ranging from 14·3% in 1988 (an unusually hot and dry season) to 36·5% in 1982 (Table V). Most of the days with suitable weather conditions occurred in May. In 2 years there were only 2 days between 1 June and 2 July that had appropriate weather conditions, although in other years there were up to 9 suitable days during June (Table V). Thus, we conclude that weather conditions promoting squeak calls occurred regularly and relatively frequently at our study site during most breeding seasons, and that these conditions were most common early in each season.

Table V. Total days with at least 2 h of suitable weather conditions for use of cliff swallow squeak calls (see text) each year between 1 May and 2 July

Year	Days (N=63) Total	%	Days in May	Days in June–July
1982	23	36·5	14	9
1983	17	27·0	9	8
1984	17	27·0	13	4
1985	14	22·2	10	4
1986	14	22·2	12	2
1987	13	20·6	11	2
1988	9	14·3	6	3
1989	13	20·6	5	8
1990	19	30·2	15	4

DISCUSSION

Cliff swallows appear to be one of the few vertebrates to possess a distinctive vocal signal that seems to be used only when food is discovered to recruit conspecifics. Other species, including toque macaques, humpback whales, chimpanzees, house sparrows, a number of galliform birds and ravens give calls associated with food that serve to attract conspecifics, although in all of these species the calls are apparently, at least occasionally, used in other contexts as well (Dittus 1984; D'Vincent et al. 1985; Elgar 1986; Goodall 1986; Marler et al. 1986; Heinrich 1988). As far as we know, the squeak call in cliff swallows is associated exclusively with the presence of food and has never been observed in other contexts. 'Food calls' in many species may simply reflect an attempt to interact on the part of the caller and may not specifically represent information about food (Marler 1967; Smith 1977). Although this interpretation cannot be ruled out for cliff swallows without controlled laboratory experiments, which are impractical, the field experiments and observations reported here strongly suggest that the squeak call does in fact convey specific information about food, and only in specific contexts.

Why should a cliff swallow call to signal its discovery of food and thus share the resource with other individuals? The most likely reason that a forager calls and shares food with conspecifics is to increase its own foraging efficiency. The dense insect swarms on which these birds often feed are ephemeral (Brown 1985a). An individual probably cannot exploit any given concentration for very long and thus incurs little cost in sharing it with conspecifics. Alerting other birds increases the number of foragers in the vicinity of the swarm, increasing the odds that the insects' subsequent movements will be tracked by at least some members of the group. Even if other birds do not also call, the caller could benefit via local enhancement simply by watching the nearby group members as some of them track the subsequent movements of the prey. Local enhancement often occurs in cliff swallows (Brown 1988b), especially during network foraging when squeak calls are most frequent. Calling to inform other foragers would be especially useful when birds are feeding nestlings and thus must commute to and from the colony and the foraging grounds. Informed foragers would track the swarm's movement while the caller goes back to its nest, enabling the caller to relocate more readily the insects upon its return to the foraging grounds.

The advantages of signalling the presence of food could be increased if calling occurs among kin, with birds selectively informing their relatives about food. Alarm-calling is known to occur selectively among non-descendant kin in several animals (e.g. Sherman 1977; Hoogland 1983), although no instances of birds selectively informing related adults about food have been reported. Heinrich (1988) rejected kin-directed benefits as the basis for food-calling in ravens since interacting individuals are almost certainly unrelated. Unfortunately, we know nothing about the kin structure of cliff swallow foraging flocks. If related adults routinely feed in proximity to each other, and thus within earshot, a forager could expect to inform kin about food whenever it called. Such a spatial organization of foraging flocks would require, however, that kin usually settle together in the same colony. This is probably unlikely for a highly migratory bird such as the cliff swallow and, so far, is not borne out by preliminary demographic analyses of this population (Brown & Brown, unpublished data).

Another possibility is that mates forage together and that birds call to inform their mates about food. This seems unlikely because calling frequently occurred early in the breeding season, probably before many birds had paired, and because members of a pair seldom if ever leave the colony together, even during periods when mate-guarding might be expected (Brown 1985a). Even if cliff swallows called to inform kin or mates, the incidental effect is to share information with substantial numbers of other conspecifics that are almost certainly unrelated.

Calling to alert conspecifics that food has been found may represent a case of 'pseudo-reciprocity' (Connor 1986; Rothstein & Pierotti 1988). Pseudo-reciprocity is characterized by interactions in which benefits returned to an original donor result from behaviour that is beneficial to the original recipient, in contrast to reciprocity in the more classical sense in which returned benefits are costly for the original recipient (Rothstein & Pierotti 1988). A caller benefits others in the foraging group by calling; by alerting others to the food source, the caller also later may receive similar benefits by watching the birds it informed track the prey or may itself be informed through others' calls. The birds that are first informed (the original recipients) pay no cost if they later call (and in fact will probably benefit). Pseudo-reciprocal interactions can arise and become established in a population relatively easily (Rothstein & Pierotti 1988). Pure reciprocity, in which the original recipient incurs a cost to reciprocate, is far less common, especially in birds (Koenig 1988), unlikely in foraging groups larger than two (Packer 1988), requires more stringent conditions to become established (Rothstein & Pierotti 1988), and hence probably cannot explain food signals in cliff swallows.

Another potential advantage of signalling food to conspecifics is that the resulting group formed at the food source may enable the caller to reduce its risk of predation (Elgar 1986). Groups are generally more likely to detect (Pulliam 1973) and possibly deter approaching predators (Robinson 1985), and an individual also may be able to use the group as a selfish herd (Hamilton 1971). Cliff swallows' squeak calls create groups, and to the degree that a group helps a caller avoid predators, the call could be considered simply a selfish anti-predator behaviour pattern. The fact that cliff swallows give the squeak call only in certain contexts (poor weather) would seem to suggest that their signals are not primarily to create selfish or vigilant herds. If predator avoidance was important, calling would also be expected in warm and sunny conditions, since predators can presumably attack under any weather conditions. Heinrich (1988) rejected anti-predator advantages as the basis for food-calling in ravens, because adult ravens have few natural predators in winter. A similar argument can be made for cliff swallows (Brown 1988b): no predators have been seen to prey on foraging adult swallows in Nebraska.

Use of squeak calls seems to be confined to relatively cool and cloudy weather, the times that aerial insects are presumably least active and hardest to find (Johnson 1969). The advantages of increased foraging efficiency during these times are clear. It is less clear, however, why these calls are apparently not used during warmer and more sunny weather. We were unable to perform playbacks at foraging sites on warm and sunny days and thus the possibility exists that squeak calls are in fact used by birds in high-altitude foraging groups under these conditions. Yet, the fact that the swallows did not use or respond to squeak calls near the colonies in warm and sunny weather (Table III) and that we seldom heard these calls in warm and sunny conditions (Fig. 2) suggests that the apparent non-use of squeak calls at those times is a real result and not an observational artefact.

Our guess is that weather exerts a major influence on the behaviour and distribution of the aerial insects on which cliff swallows feed, and this in turn affects the birds' use of squeak calls at different times. For instance, the rate of calling declined as wind speed increased, probably because wind disrupted the chironomid swarms as soon as we flushed them out of the grass. This led to a more dispersed insect distribution and, accordingly, less opportunity for the birds to track the movements of swarms. As a result, birds had less to gain from calling to recruit conspecifics. Windy conditions, therefore, should in general lead to a decrease in calling, and we never heard squeak calls used when wind speeds were greater than 32 km/h even on cool and cloudy days (although wind speeds in our study area regularly exceed 32 km/h; Wilhite & Hubbard 1989).

Perhaps the insect concentrations on which these birds feed during warm and sunny weather do not allow the same sort of tracking as in cool and cloudy weather. Alternatively, active recruitment to food during warm weather may disrupt the swarms that are active to the extent that the cost of calling is too high; Stoddard (1988) reported instances of foraging cliff swallows disrupting and dispersing insect swarms. Foragers may simply have to tolerate recruitment to insect swarms through passive means in good weather (e.g. through local enhancement) because they cannot prevent it, but they would not be expected to actively signal the presence of food during those times. Additional information on how weather affects the behaviour of the actual insect prey species (and the insects' responses to foraging swallows) is needed before we can understand fully the absence of calling under certain conditions. Acquiring this sort of information would be a formidable task, largely because cliff swallows feed on so many different insect taxa (Brown 1985a).

Advantages associated with transfer of foraging information appear to be important in the evolution and maintenance of cliff swallow coloniality (Brown 1988a, b). Active communication about food through the squeak call can be added to local enhancement and information-centre foraging (Ward & Zahavi 1973) as ways in which information is transferred in this species. We examined the effect of colony size (Table III) on the cliff swallows' responses to the squeak call, but found no differences, mostly because the swallows simply did not respond near their colonies. However, in general, colony size should affect the number of birds present on the foraging grounds, and thus the number of potential callers. As a result cliff swallows from larger colonies might be more likely to locate food via squeak calls. Active communication on the foraging grounds thus probably augments the other foraging-related advantages of cliff swallow coloniality (Brown 1988a).

The squeak call described for the cliff swallows in our study area may not be the only food signal this species possesses. Stoddard (1988) reported a rarely used tseer call in two populations of cliff swallows in Washington state, which, from verbal descriptions (Stoddard, personal communication) and in the absence of a tseer call sonagram, appears to be a very different call from the squeak call in Nebraska. The tseer call appears to be used mostly near the colony site and functions to alert the entire colony that a returning forager has found a food source nearby. Upon giving the call, the forager essentially leads the other colony members to the food. This is a seldom heard call, may occur only in small colonies, and, like the squeak call, appears to be used mostly when foraging conditions are poor (Stoddard 1988). Another call, which appears structurally more similar to the squeak call described here but nevertheless clearly different to our ears, was found in a Texas population of cliff swallows (Brown 1985a). This call, which was also referred to as a squeak call by Brown (1985a), seemed to occur in the same sorts of contexts and generated the same sort of responses as the tseer call described by Stoddard (1988). The Texas call has not been studied in any detail, however, and observations were confined to a few days in March and April, 1982 (Brown 1985a). Apparently cliff swallows may exhibit several different types of food signals used in different contexts and at varying frequencies. Further work is needed on these other calls, although as noted by Stoddard (1988), the tseer call appears to occur so rarely that it would yield a low rate of return for an investigator.

In contrast to the tseer call, the Nebraska squeak call is used relatively often. At least 20% of the days during the early and middle part of the nesting season each year have weather conditions suitable for food-calling, and in some years over a third of days are suitable. Use of this call is not a trivial and rare event. Although we lack information on foraging behaviour and social organization of cliff swallows in winter, squeak calls could be an even more important component of these birds' foraging strategies while on their wintering range and during migration, depending on the food sources used and general weather conditions at those times. Yet, despite the relative frequency of conditions that lead to use of these calls on the breeding grounds, squeak calls would be easily overlooked if the birds were studied only at their nests. Only by studying foraging cliff swallows away from their colonies (and in weather that some observers might consider too 'bad' for field work) did we discover this, at times commonly used, vocal signal. Since most researchers studying colonial birds have focused their attention on what happens at the colony sites (e.g. Wittenberger & Hunt 1985), this bias in observational effort may account in part for the overall lack of reports of food signals in other colonial species that forage socially.

ACKNOWLEDGMENTS

For field assistance we thank Barbara Calnan, Sasha Carlisle, Miyoko Chu, Kristen Edelmann, Ellen Flescher, Jerri Hoskyn, Christine Mirzayan and Craig Richman. For assistance with equipment we thank Jerri Hoskyn, Howard McCarley and the Austin College Biology Department, and the KOGA radio station in Ogallala. John Janovy, Jr, and Anthony Joern allowed us to use the facilities at the Cedar Point Biological Station, and Mathew Werner of the Department of Agricultural Meteorology at the University of Nebraska-Lincoln provided weather data. We thank Steve Beissinger, James Gibbs, Raymond Pierotti, Philip Stoddard, Bridget Stutchbury and Peter Walsh for helpful comments on the manuscript. Financial support was received from the National Geographic Society, the American Philosophical Society, and the National Science Foundation (BSR-8600608). M.L.S. thanks Ellis and Nancy Shaffer for supporting his work in Nebraska.

REFERENCES

Brown, C. R. 1985a. The costs and benefits of coloniality in the cliff swallow. Ph.D. thesis, Princeton University, Princeton, New Jersey.
Brown, C. R. 1985b. Vocalizations of barn and cliff swallows. *Southwest. Nat.*, **30,** 325–333.

Brown, C. R. 1986. Cliff swallow colonies as information centers. *Science*, **234,** 83–85.
Brown, C. R. 1988a. Enhanced foraging efficiency through information centers: a benefit of coloniality in cliff swallows. *Ecology*, **69,** 602–613.
Brown, C. R. 1988b. Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators. *Anim. Behav.*, **36,** 780–792.
Connor, R. C. 1986. Pseudo-reciprocity: investing in mutualism. *Anim. Behav.*, **34,** 1562–1566.
Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford University Press.
Dittus, W. P. J. 1984. Toque macaque food calls: semantic communication concerning food distribution in the environment. *Anim. Behav.*, **32,** 470–477.
D'Vincent, C. G., Nilson, R. M. & Hanna, R. E. 1985. Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *Sci. Rep. Whales Res. Inst.*, **36,** 41–47.
Elgar, M. A. 1986. House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Anim. Behav.*, **34,** 169–174.
Evans, R. M. 1982. Foraging-flock recruitment at a black-billed gull colony: implications for the information center hypothesis. *Auk*, **99,** 24–30.
Evans, R. M. & Welham, C. V. J. 1985. Aggregative mechanisms and behavior in ring-billed gulls departing from a colony. *Can. J. Zool.*, **63,** 2767–2774.
Goodall, J. 1986. *The Chimpanzees of Gombe*. Cambridge, Massachusetts: Harvard University Press.
Greene, E. 1987. Individuals in an osprey colony discriminate between high and low quality information. *Nature, Lond.*, **329,** 239–241.
Hamilton, W. D. 1971. Geometry for the selfish herd. *J. theor. Biol.*, **31,** 295–311.
Heinrich, B. 1988. Food sharing in the raven, *Corvus corax*. In: *The Ecology of Social Behavior* (Ed. by C. N. Slobodchikoff), pp. 285–311. San Diego: Academic Press.
Hoogland, J. L. 1983. Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*). *Anim. Behav.*, **31,** 472–479.
Johnson, C. G. 1969. *Migration and Dispersal of Insects by Flight*. London: Methuen.
Koenig, W. D. 1988. Reciprocal altruism in birds: a critical review. *Ethol. Sociobiol.*, **9,** 73–84.
Kroodsma, D. E. 1989. Suggested experimental designs for song playbacks. *Anim. Behav.*, **37,** 600–609.
Marler, P. 1967. Animal communication signals. *Science*, **157,** 769–774.
Marler, P., Dufty, A. & Pickert, R. 1986. Vocal communication in the domestic chicken: I. Does a sender communicate information about the quality of a food referent to a receiver? *Anim. Behav.*, **34,** 188–193.
Packer, C. 1988. Constraints on the evolution of reciprocity: lessons from cooperative hunting. *Ethol. Sociobiol.*, **9,** 137–147.
Pearson, T. G. (Ed.) 1917. *Birds of America. Vol. 3*. New York: University Society.
Pulliam, H. R. 1973. On the advantages of flocking. *J. theor. Biol.*, **38,** 419–422.
Robinson, S. K. 1985. Coloniality in the yellow-rumped cacique as a defense against nest predators. *Auk*, **102,** 506–519.
Rothstein, S. I. & Pierotti, R. 1988. Distinctions among reciprocal altruism, kin selection, and cooperation and a model for the initial evolution of beneficent behavior. *Ethol. Sociobiol.*, **9,** 189–209.
Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. *Science*, **197,** 1246–1253.
Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.
Smith, W. J. 1977. *The Behavior of Communicating*. Cambridge, Massachusetts: Harvard University Press.
Stoddard, P. K. 1988. The 'bugs' call of the cliff swallow: a rare food signal in a colonially nesting bird species. *Condor*, **90,** 714–715.
Ward, P. & Zahavi, A. 1973. The importance of certain assemblages of birds as 'information centres' for food-finding. *Ibis*, **115,** 517–534.
Wilhite, D. A. & Hubbard, K. G. 1989. Climate. In: *An Atlas of the Sand Hills* (Ed. by A. Bleed & C. Flowerday), pp. 17–28. Lincoln: Conservation Survey Division, University of Nebraska-Lincoln.
Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton, New Jersey: Princeton University Press.
Wilson, E. O. 1971. *The Insect Societies*. Cambridge, Massachusetts: Harvard University Press.
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.
Wrangham, R. W. 1986. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: *Primate Ecology* (Ed. by T. H. Clutton-Brock), pp. 503–538. London: Academic Press.