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ENHANCED FORAGING EFFICIENCY THROUGH INFORMATION CENTERS: A BENEFIT OF COLONIALITY IN CLIFF SWALLOWS¹

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Abstract. Cliff Swallows (Passeriformes: *Hirundo pyrrhonota*) in southwestern Nebraska, USA, nest in colonies that serve as information centers in which unsuccessful individuals locate and then follow successful individuals to aerial insect food resources. I investigated to what degree colony size affected the efficiencies at which Cliff Swallows foraged for food, and to what degree information transfer among colony residents might represent a benefit of living in colonies. The number of Cliff Swallows departing from a colony each hour to forage increased significantly with colony size, meaning that individuals did not wait as long to locate appropriate foraging associates in large colonies as in small colonies. Waiting intervals between an individual's arrival at its nest and its departure on its next foraging trip increased as the number of birds nesting in a colony declined. Parental Cliff Swallows in large colonies returned with food for their nestlings more often and brought more food per trip, than did parental Cliff Swallows in small colonies. As a result, nestling body mass at 10 d of age increased significantly with colony size, when the confounding negative effects of ectoparasites on nestling body mass were removed by fumigating nests. Adult Cliff Swallow body mass late in the nesting season during the period of feeding of nestlings increased significantly with colony size even in the presence of blood-sucking ectoparasites (in nonfumigated colonies). Experimental reduction of large Cliff Swallow colonies to the approximate size of small colonies suggested that nestling and adult body mass in these colonies did not vary with colony location, meaning that enhanced foraging efficiency of birds in larger colonies was probably attributable to more efficient transfer of information among the larger number of colony residents and was probably not attributable to differences in local resource characteristics near colonies of different sizes. Enhanced foraging efficiency through information centers is likely a major benefit of coloniality for Cliff Swallows.

Key words: Cliff Swallow; coloniality; fitness; foraging; *Hirundinidae*; *Hirundo pyrrhonota*; information center; Nebraska; reproduction; social behavior.

INTRODUCTION

One potential benefit of living in a group is the opportunity to increase one's foraging efficiency by observing where other individuals successfully locate food. Regular return to a fixed location, such as a breeding colony of birds, may allow an unsuccessful individual to cue on the success of a returning forager and subsequently follow that forager to prey (e.g., Ward and Zahavi 1973, Waltz 1982). If animals living in groups can thus enhance their foraging efficiency, information transfer among colony residents via an "information center" might represent a major benefit of coloniality.

The existence of information centers in nonhuman vertebrates is problematical. Although the phenomenon is well documented in social insects (e.g., von Frisch 1967, Wilson 1971, Seeley 1985), most of the evidence for information centers in vertebrates (mainly birds) is inconclusive or negative (e.g., Bayer 1982, Wittenberger and Hunt 1985). However, I have documented the existence of information centers in a colonial bird,

the Cliff Swallow (*Hirundo pyrrhonota*) (Brown 1986). Cliff Swallows live in colonies of up to 3000 nests, and while individuals are feeding nestlings, they follow each other to locate ephemeral patches of flying insects. A Cliff Swallow that has been unsuccessful on a recent foraging trip identifies a successful forager, apparently mainly by observing the food it brings back in its bill and throat, and then follows that successful individual from the colony to a foraging location (Brown 1986).

It is unknown whether information transfer varies with colony size. With more individuals present in large colonies, an unsuccessful individual in a large colony might more rapidly locate an appropriate successful individual to follow to a food source (Hoogland and Sherman 1976). This could enhance foraging efficiency and lead to enhanced nestling growth rates and greater fitness for birds in large colonies. This paper's goal is to explore the effects of colony size on foraging efficiencies of individual Cliff Swallows as a measure of the benefits associated with information centers.

Greater foraging efficiency of birds nesting in large colonies could also reflect local differences in food abundance. Food could be unevenly distributed, and

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large colonies might form in particularly rich sites. This factor could account for colony size-specific variation in foraging efficiency independent of any effects of information centers. The effects of local food abundance on the structuring of avian colony sizes have not been examined either theoretically or empirically (see Wittenberger and Hunt 1985). This paper also explores whether any effects of colony size on Cliff Swallows' foraging efficiencies might be explained by variation in local resource abundance.

STUDY ANIMAL AND STUDY SITE

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 ≈ 3000 m, but rarely at higher altitudes (Grinnell and 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 (A.O.U. 1983). The birds build gourd-shaped nests out of mud pellets, and their 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 hematophagous ectoparasites are responsible for much of the observed nestling mortality (Brown and Brown 1986). The Cliff Swallow's general biology has been well studied (Emlen 1941, 1952, 1954, Mayhew 1958, Samuel 1971, Grant and Quay 1977, Withers 1977, Brown 1984, 1985).

This study, part of continuing long-term research on the social behavior of Cliff Swallows, was conducted in southwestern Nebraska, USA, 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 likely increased in recent years with the construction of artificial structures upon which they can nest. However, these birds 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). 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, there were 218 Cliff Swallow colonies totalling 70 545 nests in or near the study area in Keith, Garden, and Lincoln counties (Brown 1985). Colony size ranged from 2 to 3000 nests ($\bar{X} = 323.6$, $SD = 510.0$), and birds also nested solitarily. The most common colony size was ≈ 350 nests.

METHODS

General procedures and definitions

Colonies chosen for intensive study were all of those within 15 km of the Cedar Point Biological Station unless the nature of a colony site there made access by us dangerous or impossible. Three additional, particularly accessible sites 20–45 km away were also studied intensively. Study colonies were named and, where possible, all nests were numbered and their progress followed throughout the nesting season. In large colonies, we could study only a sample of the nests, and in these cases we selected nests from all accessible parts of the colony. We reached Cliff Swallow nests with aluminum ladders, or canoed, swam, or waded to the bases of cliff sites or into culverts, where ladders were unnecessary. Nests were marked by writing chalk numbers on the nearby concrete substrate (for colonies using bridges or culverts) or by driving nails with numbered heads into the cliff face (for cliff colonies). All nests were checked each day or every 2–3 d until hatching in a colony started, at which time we began checking nests every day or every other day. We observed nest contents with a dental mirror and a small flashlight inserted through each nest's mud neck. It was occasionally necessary to chip away pieces of dried mud from the neck to insert the mirror, but it was not necessary to alter the nest appreciably, and birds quickly repaired any damage. Cliff Swallows continually added fresh mud to all nests, those studied and those not studied, suggesting that repair brought on by our activity did not lead to much additional energy or time demands on the birds. Removal of small amounts of mud from the necks of Cliff Swallow nests has little adverse effect on the birds' reproductive success (Hamilton and Martin 1985, C. R. Brown, *personal observation*). Once all eggs of a Cliff Swallow clutch hatched, we did not disturb that nest again until the 10th d after hatching, at which time we recorded the number of nestlings present and the body masses of the nestlings (see Recording Body Mass).

"Colony size" in this paper refers to the number of active nests and does not include unused nests, which

occurred commonly in many colonies. For most colonies, size remained largely constant throughout the nesting season, but whenever appreciable numbers of pairs lost their clutches and deserted the colony due to natural causes or as a result of our colony reduction experiment (see Colony Reduction Procedures), we used the smaller colony sizes for calculations involving those colonies later in the season. In most cases neighboring colony sites were separated by at least 1 km, and often > 15 km. For small colonies located in a network of highway culverts, nests were considered to represent a separate colony if the nest substrate upon which they were located was not physically connected to another nest-group's substrate, or if at least 25 m of unoccupied substrate separated them from the nearest group of nests; and if nest owners used a culvert entrance whose orientation was predominantly different from that of neighboring nests. Our observations at these culvert sites suggested that owners of nests distinguished by these criteria rarely, if ever, interacted with each other and thus probably belonged to separate colonies. For colonies located on cliff sites, groups of nests were treated as separate colonies if separated by at least 75 m of substrate obviously unsuitable for nest attachment. Owners of nests distinguished by this criterion seldom interacted with each other.

Since hematophagous ectoparasites severely reduce nestling Cliff Swallow body mass and survivorship (Brown and Brown 1986), parts of some, and some entire, colonies were fumigated with an insecticide to kill ectoparasites. Fumigation procedures are described in Brown and Brown (1986). Fumigation was totally effective against swallow bugs (*Oeciacus vicarius*; Hemiptera: Cimicidae), the major Cliff Swallow ectoparasite; none was found on nestlings in fumigated nests (Brown and Brown 1986). Fumigated nests thus represented samples with no potentially confounding effects of ectoparasitism on nestling growth and survivorship.

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. Whenever data were not normally distributed, nonparametric statistical tests were used (Siegel 1956).

Scoring departure frequencies and waiting intervals

We recorded how frequently birds departed from colonies of different sizes, and timed the interval between a bird's arrival at its nest and its subsequent departure on its next foraging trip, as a measure of how rapidly individuals might locate other individuals to follow to food sources. During 1983–1984, in colonies ranging up to 345 nests in size, we timed with stopwatches the intervals between all departures and arrivals of Cliff Swallows on dates on which virtually all

individuals within the colonies were feeding nestlings (see Brown 1985). These data resulted in a continuous time record of all departures at each colony, since the time of each departure was recorded to the nearest second. We then calculated the total number of seconds per hour on which at least one Cliff Swallow departed from each colony. Only hours for which we had a continuous time record for all 3600 s and during which the birds were undisturbed by people or predators, were used. At a 2000-nest colony it was physically impossible to time intervals between departures, and there we simply recorded the cumulative seconds on which at least one bird departed from the colony. Total time of observations of this sort at each colony ranged from 1 to 23 h.

At a 165-nest colony in 1983, we observed individual Cliff Swallows feeding nestlings and timed with stopwatches the interval elapsing between their feeding of their nestlings or, for birds returning without food, their arrival at the nest, and their next departure toward the foraging grounds. Only birds feeding relatively large nestlings (≥ 10 d old), which partially or entirely blocked the entrance to the enclosed nest and thus kept the parents clinging to the nest's exterior in full view, were observed (see Brown 1986). Using this procedure, we could determine accurately when the parents arrived and/or actually fed the nestlings, and thus we knew when to begin timing. Timing ended when the parent flew from the nest.

Related data on the effect of group size on waiting intervals were recorded at a 13-nest colony in 1983 where departing Cliff Swallows often repeatedly circled above the colony before flying to a foraging site. We recorded whether individuals left their nests as a group (defined as two or more birds departing within 5 s of each other [Brown 1986]) or whether they left individually, and then whether they made at least one 360° circle of the colony before flying to a foraging site. This colony was located in open, treeless terrain, and thus we could observe with binoculars all foraging by colony residents in the surrounding fields and could easily see whether Cliff Swallows circled the culvert entrance. We did not time the duration of the period in which Cliff Swallows circled the colony. We watched for similar circling behavior by Cliff Swallows at other, larger colonies located in equally open terrain. To avoid possible differences in interpretation of behavior that constituted "circling," only one person watched for circling behavior in the different colonies.

Counting food deliveries

We examined how often Cliff Swallows in different-sized colonies delivered food to their nestlings. For periods of 1 h, we counted the total number of food deliveries made by parents at focal nests. We counted only visits to the nests in which nestlings were actually fed by adults (i.e., food deliveries). Times when parental Cliff Swallows returned to their nests after ap-

parent unsuccessful foraging were not recorded because we wanted a measure of parents' foraging success in different-sized colonies. By scoring only visits in which food was delivered, we also minimized the chances of ever scoring a visit by a nonparental bird, since known color-marked Cliff Swallows were never seen feeding nestlings at a nest other than their own. Using one person as an observer and one person as a data-recorder, up to 45 focal nests at a time could be thoroughly watched and all food deliveries counted. When only one person was available to watch and to record data, only up to ≈ 20 nests could be watched at a time without missing any visits. Cliff Swallows habituated quickly to our presence, and birds could be observed easily from distances of ≈ 10 m without need of a blind. For each nest watched, we recorded age and number of nestlings present.

Most nests were watched for multiple hour-long periods and on different days, but since each hourly watch was not statistically independent, counts at each nest were averaged and statistical analyses based on nest means. These data were collected on the same days and during the same periods of time (usually 0800 to 1200 Mountain Daylight Time [MDT]) at the different colonies by separate teams of observers, so that there were no presumed seasonal or circadian influences on prey availability between sites. Observations were confined to nests in which nestlings were 10 or more days old, in which parents seldom completely entered the nests to feed their nestlings, and thus we could see if the adult birds carried food. Parental Cliff Swallows with food were obvious (see Brown 1986). Although all nests containing broods of from one to five nestlings were watched, because of small sample sizes, broods of one and five nestlings were excluded from the analyses.

Ring-collaring nestlings

Food boluses fed to nestling Cliff Swallows were collected to measure the amount of food delivered to nestlings in colonies of different sizes. Ring-collaring techniques followed those of Orians and Horn (1969), in which a pipe cleaner was placed around a nestling's neck to prevent swallowing of food boluses. Prey samples were thus collected intact. Ring-collaring is not harmful to nestlings if collars are adjusted correctly, and this procedure does not normally affect nestling growth rates (Henry 1982). We selected nests containing nestlings from 10 to 16 d old, and usually collared at least half of the nestlings in a nest at any one time. We used only brood sizes of three and four nestlings for ring-collaring. We left nestlings collared for ≈ 20 min in most cases, and never collected more than one sample per day from any one nestling. Parental Cliff Swallows delivered tightly compressed boluses (as in other swallow species [Turner 1982]), always to only one nestling per visit, and boluses seldom came apart

even slightly, allowing us to collect all food delivered at a visit. Parents seemed never to feed a nestling that already had a bolus lodged in its throat. We collected boluses from the nestlings' throats with forceps, placed each sample in 70% alcohol, and returned to the laboratory where each bolus's wet mass was recorded to the nearest 0.01 g and the insects contained in the bolus were identified to family.

Recording body mass

We recorded body mass of nestling and adult Cliff Swallows in colonies of different sizes to examine how nestling growth rates and adult condition might reflect differences in foraging efficiencies. For each nest, body masses of the nestlings were recorded with a 50-g Pesola scale on the 10th d after hatching (hatch date = day 1). Day 10 was selected because that is the time of maximum gain in nestling body mass for Cliff Swallows (Stoner 1945). We wanted a measure of the degree to which nestling growth reflected parental foraging success (e.g., Hoogland and Sherman 1976, Snapp 1976). Since data from nestlings within the same nest were not statistically independent, we averaged body masses for all nestlings within each nest and examined the mean body mass per nestling per nest. All nestlings were banded for permanent identification with standard United States Fish and Wildlife Service bands. At day 10 it was necessary to remove parts of the mud necks of some nests to extract nestlings. Since Hamilton and Martin (1985) reported that removal of entire necks from Cliff Swallow nests may reduce reproductive success and constitute a major form of interference, we rebuilt all nests with mud. The swallows added to our repair jobs with mud of their own.

Adult Cliff Swallows were captured in mist nets that were strung across the entrances to culverts containing colonies or that were dropped by us from the tops of bridges under which swallows nested. Adult body mass was recorded with a 50-g Pesola scale. Most adult body masses were recorded between 0800 and 1600, MDT. There was no consistent pattern of change in body mass with time of day (C. R. Brown, *personal observation*); thus all body masses were used irrespective of the hour in which the birds were caught. Sexes of adults were not recorded in 1984–1985, the years from which our data on adult body mass came. Each adult was banded with a standard United States Fish and Wildlife Service band, and some birds were color-marked by painting their white foreheads (see Brown 1984). Some individuals were caught more than once; we arbitrarily used the first body mass recorded for those individuals. Adults were captured early in the season and again later in the season when feeding nestlings. Adult Cliff Swallows captured early in the season had just arrived in the study area and were establishing ownership of nests. All early-season body masses were taken in mid to late May 1984. Later in the season, body masses of

adult Cliff Swallows were recorded when at least half of all nests contained nestlings at least 10 d old. Using this criterion assured that almost all birds in each colony were feeding at least newly hatched nestlings when captured, since nesting within Cliff Swallow colonies in Nebraska is highly synchronized (Brown 1985). Most of the late-season body mass data were recorded during the last two weeks of June and the first week of July, 1984–1985. Birds could be captured quickly at most colonies, and adequate sample sizes could be obtained during about a 2-d period of netting at each colony.

Colony reduction procedures

In 1985 Cliff Swallow colonies were experimentally reduced in size to examine the potential effects of local food abundance on individuals' foraging efficiencies (see Results). Three Cliff Swallow colonies were selected, and these were reduced by us to the approximate sizes of four smaller, unaltered, "control" colonies (Table 1). Reduction occurred after laying had ceased and before hatching had started in each colony (Table 1). Nests to be removed were randomly selected from all parts of the colonies, and the bottoms of these nests were cut out with a knife. The sides and tops of these nests remained on the substrate to prevent any potential spatial confusion over nest locations by large numbers of birds that lost their nests or by the birds whose nests remained. Slicing away the bottoms of these nests resembled natural nest breakage events. Upon loss of their eggs and part of their nests, most nest owners immediately left the colony. In a few instances Cliff Swallows tried to repair their nests and re-lay, but we continued to break away any new mud they added to these nests. Thus, we maintained all reduced colonies at the designated size throughout the nesting season. Removal of nests was sufficient to reduce effectively the numbers of adult Cliff Swallows present at the colonies, and no adult birds were killed or removed. Data on nestling and adult body mass were recorded in the reduced colonies and in the unaltered control colonies, as described earlier.

TABLE 1. Original and final sizes, and phenology, of Cliff Swallow colonies that were reduced in size and of others that served as unaltered controls, 1985.

Original colony size (no. active nests)	Modal clutch initiation date*	Date reduced	Final colony size (no. active nests)
41	30 May	n.r.†	41
42	19 May	n.r.	42
42	21 May	n.r.	42
44	11 June	n.r.	44
81	17 June	30 June	61
90	18 May	4 June	54
120	20 May	7 June	63

* Single date on which the most clutches were initiated in the colony.

† n.r. = not reduced.

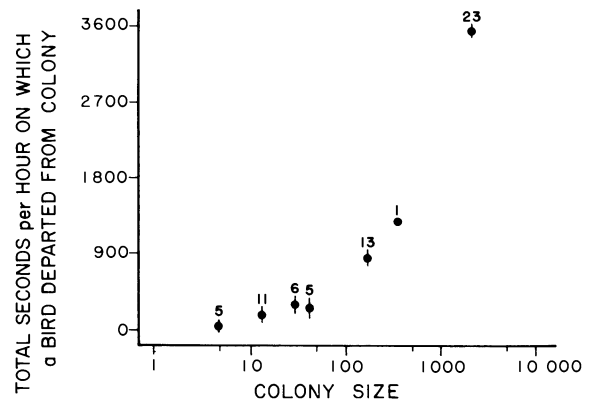


FIG. 1. Total number of seconds per hour on which at least one Cliff Swallow departed from the colony vs. colony size (number of active nests). Means \pm 1 SE shown. Total number of hours scored for each colony size is shown above SE bars. Total seconds per hour on which at least one bird departed increased significantly with colony size ($r_s = 0.96$, $P < .001$).

RESULTS

Departure frequencies and waiting intervals vs. colony size

A large colony might provide more foraging information to an individual than might a small colony simply because the greater number of conspecifics in a large colony insures that some individuals will often be leaving the colony to forage. An unsuccessful forager might therefore more readily locate a departing successful forager in a large colony at any given time.

For colonies ranging in size from 5 to 2000 nests, the number of Cliff Swallows departing each hour to forage increased significantly with colony size as expected (Fig. 1). At a colony of 2000 nests, birds departed virtually continuously (Fig. 1). These data confirm intuitive reasoning that unsuccessful Cliff Swallows in large colonies might have more opportunities to locate appropriate individuals to follow and thus waste less foraging time, than birds in small colonies.

Birds nesting late in the season might have reduced opportunities to glean information from other colony residents, as earlier nesting individuals *within* the colony finish and depart (Emlen and Demong 1975). At a 165-nest colony, we examined the effect of diminishing colony size during the season on the length of time between the arrival of individuals at the nest and departure on the next foraging trip. This interval probably reflected the time spent looking for foraging associates both by previously successful and unsuccessful individuals. During this interval, focal individuals scanned continuously, apparently for other departing birds. At this colony prior to 5 July 1983, virtually no nestling Cliff Swallows had fledged. Between 5 and 8 July, a rash of fledgings occurred. As large numbers of juveniles and their parents departed, the colony was reduced in size from 165 to 75 active nests over a 4-d period.

TABLE 2. Duration of period that Cliff Swallows waited after arrival at the nest and before departing on the next foraging trip, as the colony size diminished.

Date	Colony size	Waiting interval (s)*		N (no. of intervals)
		\bar{X}	SE	
4 July 1983	165	1.46	0.21	182
5 July 1983	160	1.33	0.21	139
6 July 1983	114	4.84	0.52	136
8 July 1983	75	4.44	0.53	196

* Intervals on 4-5 July (before the colony size diminished) were significantly shorter than intervals on 6-8 July (after the colony size diminished) (Mann-Whitney *U* test, $z = -10.72$, $P < .001$).

During this period we recorded waiting intervals for nest owners in a sample of 46 focal nests. We thus collected data from the same individuals at the same site, both before and after the colony decreased in size. Intervals between arrival at the nest and departure on the next foraging trip increased by about a factor of 3 when the colony size decreased (Table 2). This result suggests that time spent looking for foraging associates may increase for individuals nesting late in Cliff Swallow colonies.

In addition to waiting and scanning for other birds while perched at their nests, Cliff Swallows also waited by circling above their colonies. At a 13-nest colony, individuals sometimes departed from their nests and made 360° circles around the colony site. This behavior would continue for up to several minutes, usually until another individual or a group of Cliff Swallows departed from the colony in a direct, straight flight toward a foraging site. The circling individual(s) would then immediately follow the straight-flying individual or group. Sometimes up to three different Cliff Swallows, all leaving their nests at different times, would assemble in "circling patterns" above the colony until another bird or a group of birds departed from the colony in direct flight, whereupon the circlers would follow.

Solitary Cliff Swallows that left their nests were more likely to circle the colony than were departing groups of birds (total solitaries departing = 328, solitaries that circled = 234 (71.3%); total groups departing = 169, groups that circled = 23 (13.6%); $\chi^2 = 148.8$, $P < .001$). Departing groups were likely to go straight toward a foraging site. These observations suggest that the more often an individual Cliff Swallow is able to depart as part of a group (i.e., follow a simultaneously foraging individual), the less foraging time it wastes. In large colonies (i.e., ≥ 165 nests) where departures were frequent (Fig. 1), we never saw Cliff Swallows circle in apparent attempts to locate foraging associates.

Number of food deliveries vs. colony size

The preceding results suggested that individual Cliff Swallows in large colonies more readily located individuals with whom to forage and wasted less foraging

time than did individuals in small colonies. These observations, therefore, led us to predict that parental Cliff Swallows in large colonies might deliver more food to their nestlings per unit time than would parental Cliff Swallows in small colonies.

For broods of 2-4 nestlings 10-17 d in age, we counted the number of food deliveries per hour made by both parents at focal nests in an 85-nest colony and in a 456-nest colony. A food delivery was any visit to the nest by a parent with food. For these brood sizes and ages, surprisingly, food delivery rates did not vary significantly with either nestling age (ANOVA: $F = 1.05$; $df = 7, 150$; $P > .05$) or with brood size (ANOVA: $F = 1.19$; $df = 2, 38$; $P > .05$). We thus pooled food delivery rates for all nests regardless of brood size or age. Significantly more food deliveries per hour were made to nests in the large colony ($\bar{X} = 15.00$, $SE = 0.56$, range 5.33 to 25.50 deliveries/h, 476 hourly watches, $N = 42$ nests) than in the small colony ($\bar{X} = 9.80$, $SE = 0.63$, range 3.00 to 24.00 deliveries/h, 428 hourly watches, $N = 41$ nests) (Mann-Whitney *U* test, $z = -5.68$, $P < .001$). This result suggests that foraging time saved by individual Cliff Swallows in the large colony (by readily locating foraging associates) translated into more food deliveries per unit of time, relative to the number of food deliveries in the small colony. There was no evidence that age (and thus experience) of foragers within a colony varied with colony size (C.R. Brown, *personal observation*). These two colonies were synchronized in time, and size appeared to be the only major difference between them.

Amount of food delivered vs. colony size

Even though parent Cliff Swallows in the large colony visited their nests to deliver food more often than did parent Cliff Swallows in the small colony, the net

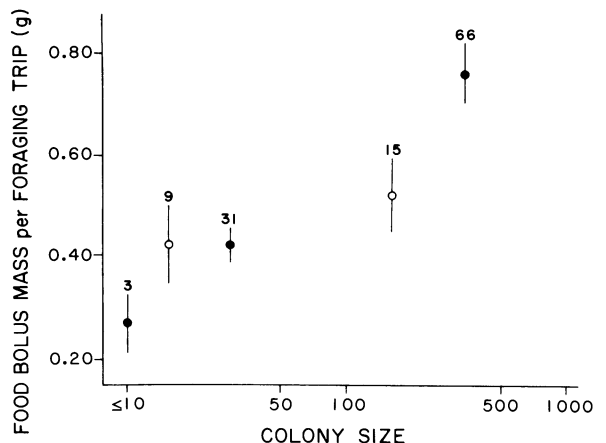


FIG. 2. Mass of food boluses (g) fed to nestling Cliff Swallows per foraging trip vs. colony size (number of active nests), 1983 (O) and 1984 (●). Means ± 1 SE shown. Total number of boluses sampled shown above SE bars. Bolus mass per trip increased significantly with colony size ($r_s = 0.42$, $P < .001$).

amount of food delivered could still be similar if birds in small colonies returned with more food per visit. We examined whether the amount (mass) of food per delivery varied with colony size.

Food boluses were collected from ring-collared nestlings in broods of 3–4 nestlings that were of the same ages as the broods in the observations on food delivery rates. Food bolus mass increased significantly with colony size (Fig. 2). Parent Cliff Swallows in the largest colony returned with, on average, almost 0.5 g more food per delivery than did Cliff Swallows in the smallest colony (Fig. 2). These results are consistent with the hypothesis that savings in foraging time in large colonies (by often being able to follow other birds to food sources without delay) allow individuals to gather more prey per trip.

Nestling body mass vs. colony size

Data in preceding sections suggested that parent Cliff Swallows in large colonies delivered larger loads of food more often than did the birds in small colonies. This increased amount of food might translate into enhanced nestling growth rates and enhanced nestling survivorship and reproductive fitness for birds in large colonies relative to that for birds in small colonies. However, simple correlations of nestling growth parameters with colony size are misleading in part because of increased ectoparasitism in the larger colonies. Infestations of hematophagous swallow bugs increase with Cliff Swallow colony size and depress nestling body mass and survivorship (Brown and Brown 1986). Since the costs of ectoparasitism and the presumed benefits of enhanced foraging efficiencies varied together with colony size, we removed the confounding effects of ectoparasites. This was done by fumigating

TABLE 3. Body mass of nestling Cliff Swallows at 10 d of age for broods of 2–4 nestlings in three fumigated colonies of different sizes, 1986.

Brood size	Colony size (no. active nests)	Body mass per nestling (g)*		N (no. broods)
		\bar{X}	SE	
2	140	21.01	0.90	8
	163	21.92	0.90	9
	750	23.56	0.27	83
3	140	21.46	0.46	23
	163	21.93	0.38	22
	750	23.40	0.15	185
4	140	21.26	0.35	44
	163	19.58	0.63	5
	750	22.46	0.16	140

* Body mass of nestlings in the 750-nest colony was significantly greater than body mass of nestlings in either the 140-nest colony or the 163-nest colony for brood sizes of two nestlings ($t = 2.81$ and 1.99 , $P < .01$ and $P < .05$, respectively), for brood sizes of three nestlings ($t = 4.14$ and 3.15 , $P < .001$ and $P < .01$, respectively), and for brood sizes of four nestlings ($t = 3.46$ and 3.33 , respectively, $P < .001$ for both).

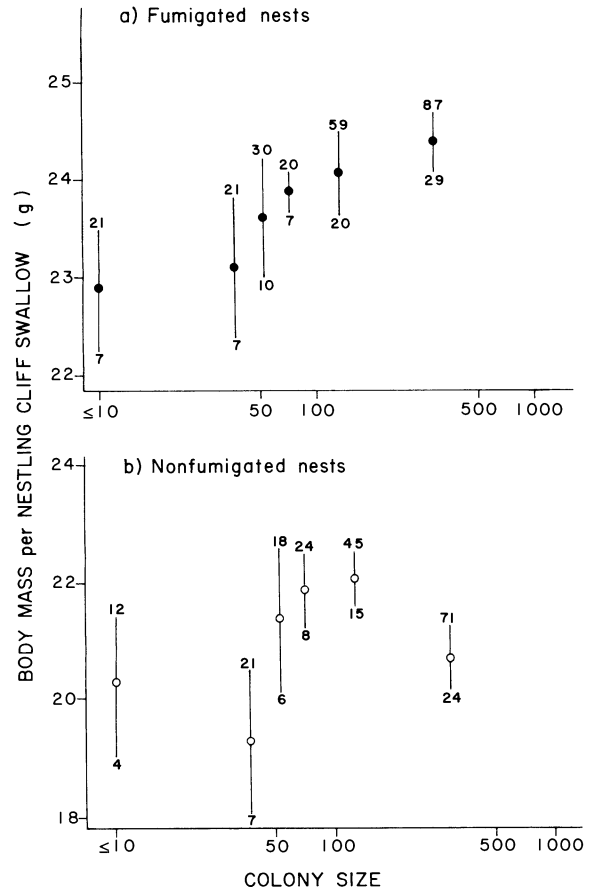


FIG. 3. Body mass (g) of nestling Cliff Swallows at 10 d of age vs. colony size (number of active nests) for (a) fumigated nests in which the effects of ectoparasites were removed, and (b) nonfumigated nests, 1984. Only broods of three nestlings were included for each. Means \pm 1 SE shown. Total number of nestlings and total number of nests sampled for each colony size shown above and below SE bars, respectively. Body mass per nestling in fumigated nests increased significantly with colony size ($r_s = 0.22$, $P = .023$). There was no significant correlation between body mass per nestling and colony size for nonfumigated nests ($r_s = -0.09$, $P = .230$).

nests (Brown and Brown 1986), resulting in colonies where the possible benefits associated with enhanced foraging efficiencies were not masked by ectoparasitism.

Body mass of nestling Cliff Swallows at 10 d of age increased significantly with colony size in fumigated nests in 1984 (Fig. 3a). Similarly, body mass of nestling Cliff Swallows at 10 d of age in a fumigated 750-nest colony in 1986 was significantly greater than body mass of nestlings in two smaller fumigated colonies that year (Table 3; the relevant comparison for each brood size is between the 750-nest colony and the two smaller colonies of roughly equivalent size). Although the 1984 data (Fig. 3a) came only from broods of three nestlings (we had the most adequate sample size for this year and brood size), the pattern of heavier nestlings in the

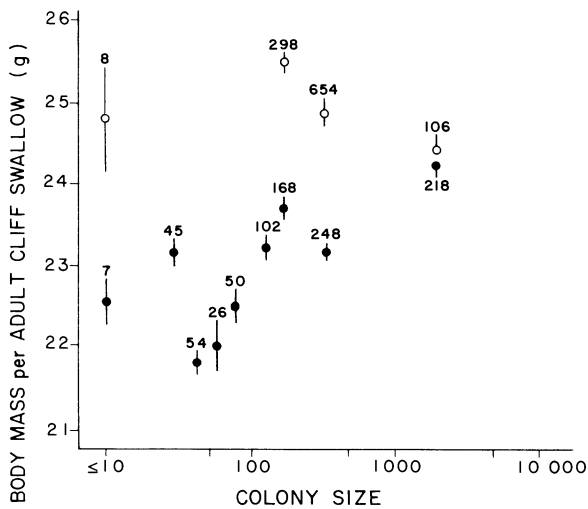


FIG. 4. Body mass per adult Cliff Swallow (g) vs. colony size (number of active nests), taken early in the season when birds were first arriving (○) and during feeding of nestlings (●), 1984. Means \pm 1 SE shown. Number of birds sampled for each colony size shown above SE bars. Body mass per adult declined significantly with colony size early in the season ($r_s = -0.20$, $P < .001$). Body mass per adult increased significantly with colony size during the nestling feeding period ($r_s = 0.28$, $P < .001$).

largest colony held also for brood sizes of two and four nestlings in 1986 (Table 3). These data show that, when the effects of ectoparasites were removed, nestling Cliff Swallows in large colonies grew faster and had greater body masses than nestlings in small colonies. Interestingly, had we not removed the effects of ectoparasites, this relationship would indeed have been masked, because in nonfumigated nests of these colonies nestling body mass did not increase significantly with colony size (Fig. 3b).

Adult body mass vs. colony size

Enhanced foraging efficiency in larger Cliff Swallow colonies might also affect the body mass and physical condition of the foragers themselves, that is, the adult birds. We examined whether adults occupying large colonies had greater body masses and thus were perhaps in better physical condition than adults in small colonies. Ectoparasites' effects on adult Cliff Swallows are unknown (Brown and Brown 1986), but may be less severe than on nestlings, because adults spend less time inside the nests than do nestlings. Thus, we used nonfumigated colonies to examine the effect of colony size on adult body mass.

A potentially confounding factor in an analysis of the relationship between adult Cliff Swallow body mass and colony size could be initial settlement patterns of birds when first arriving in the spring. If large colonies are superior and therefore heavier birds tend to settle there first, due perhaps to these individuals' greater competitive abilities, adult body mass might not reflect

any effects of foraging enhancement. However, in our sampling of adult body mass early in the season, we found no indication that heavier birds tended to settle in larger colonies at the start of the nesting season (Fig. 4). There was a hint that heavier birds might even choose smaller colonies early in the season. However, by the end of the nesting season adult body mass increased significantly with colony size (Fig. 4). In four colonies we sampled body masses of adults both early and late in the season, and in the three smaller of these colonies, individuals had dropped ≈ 2.0 g in mass, on average, by the end of the nesting season. Individuals in the largest colony had remained at nearly their pre-breeding body mass throughout the nesting season (Fig. 4), despite the presumed stresses of feeding nestlings and the greater numbers of ectoparasites in the larger colonies. These results suggest that adult Cliff Swallows in large colonies are in better physical condition than adults in small colonies by the end of each nesting season.

Potential effects of local food resources on nestling and adult body mass

More frequent food deliveries to nests in large colonies, more food delivered per visit in large colonies (Fig. 2), enhanced nestling growth in large colonies (Fig. 3a, Table 3), and enhanced adult body mass in large colonies at the end of the nesting season (Fig. 4), could all result if large Cliff Swallow colonies tended to be located near particularly abundant or densely concentrated food resources. If food resources were sufficiently better near large colonies than near small colonies, these colony size effects could occur without any foraging enhancement via information centers.

Because Cliff Swallows in Nebraska feed on such a diversity of aerial insect prey (Brown 1985), direct sampling of food resources near colonies is difficult. We therefore used an alternative approach in which we reduced the sizes of large Cliff Swallow colonies, thus removing many potential foraging associates for the individuals that remained. If large colonies form near abundant food resources and the colony size effects documented earlier merely reflect the locations of colonies of different sizes, the same results we documented in preceding sections should occur even when the numbers of birds at the large colony sites are reduced. If, on the other hand, the colony size effects documented earlier are attributable to efficient information transfer among the many residents in large colonies, when the large colonies are reduced we should observe no differences in these parameters between the birds remaining at the formerly "large" colonies and the birds living in small, unaltered colonies of similar size.

Large Cliff Swallow colonies were reduced in size by removing nests (see Methods: Colony Reduction Procedures). Colonies were not reduced until all laying there had ceased and the birds had thus "committed" themselves to a colony of that size at that site (Table

TABLE 4. Body mass of nestling Cliff Swallows at 10 d of age for broods of 2–4 nestlings in fumigated colonies that had been reduced in size (*) and in fumigated, unaltered, "control" colonies, 1985.

Brood size	Colony size* (no. active nests)	Body mass per nestling (g)†		N (no. broods)
		\bar{X}	SE	
2	41	23.67	0.75	7
	42	24.80	1.10	5
	42	22.03	1.77	6
	44	24.31	0.53	7
	54*	22.80	0.00	1
	61*	24.30	0.78	12
	63*	21.28	1.32	5
3	41	23.91	0.83	7
	42	23.42	1.52	5
	42	22.32	0.98	13
	44	23.32	0.61	11
	54*	22.52	0.57	20
	61*	23.97	0.57	16
	63*	24.26	0.48	15
4	41	23.14	0.59	13
	42	22.95	0.51	15
	42	22.41	0.43	12
	44	22.42	0.59	5
	54*	21.64	0.40	31
	61*	22.96	0.47	16
	63*	22.72	0.38	30

* Final colony sizes of reduced colonies (see Table 1).

† Body mass per nestling did not vary significantly with either brood size or colony size (Kruskal-Wallis two-way ANOVA, $H = 2.39$, $P = .118$).

1). Colonies chosen for reduction were large enough to expect (before reduction) many of the previously described colony size advantages to occur (e.g., Fig. 2, Fig. 3a). An effort was made to reduce the large colonies to the same sizes as the small "control" colonies, but in reality the reduced colonies remained on average $\approx 40\%$ larger than the control colonies (Table 1). Because of the previously documented effects of ectoparasites, all reduced colonies and all control colonies were entirely fumigated to remove confounding effects of swallow bugs.

Body mass of nestling Cliff Swallows at 10 d of age did not vary significantly with either brood size or

TABLE 5. Body mass of adult Cliff Swallows while feeding nestlings in fumigated colonies that had been reduced in size (*) and in fumigated, unaltered, "control" colonies, 1985.

Colony size* (no. active nests)	Body mass per adult (g)†		N (no. birds)
	\bar{X}	SE	
41	22.21	0.27	45
42	22.99	0.24	46
44	22.50	0.16	34
54*	21.97	0.19	64
61*	23.26	0.25	51
63*	22.43	0.17	64

* Final colony sizes of reduced colonies (see Table 1).

† Body mass per adult did not vary significantly with colony size (Kruskal-Wallis one-way ANOVA, $\chi^2 = 3.39$, $P > .05$).

colony size for the colonies in the reduction experiment (Table 4). Body mass of adult Cliff Swallows while feeding nestlings in these colonies did not vary significantly with colony size (Table 5). These results indicate that nestling growth rates and adult body mass were not enhanced in large colonies that were reduced in size, relative to small colonies. The reduced colonies were still $\approx 40\%$ larger than the controls and thus biased this experiment toward finding colony size effects. That none was found strengthens the conclusion that reduced and control colonies did not differ (Tables 4 and 5).

DISCUSSION

This study suggests that individual Cliff Swallows in large colonies forage more efficiently than do individuals in small colonies. Foraging may be enhanced because individuals in large colonies can more readily locate appropriate individuals with which to forage, leading to increased amounts of food delivered to nestlings and to increases in nestling growth rates and adult body mass. The colony reduction experiment suggests that these colony size effects are not attributable to features of local food resources near small vs. large colonies, but instead may result from increased opportunities to transfer foraging information among conspecifics in the larger colonies.

Why might large Cliff Swallow colonies be more efficient information centers than small ones? Unsuccessful Cliff Swallows often cue on the foraging success of their close neighbors within the colony (Brown 1986), suggesting that once colony size reaches some (relatively small) size threshold in which all individuals have equal numbers of close neighbors, further increases in colony size might not further enhance an individual's foraging efficiency. However, Cliff Swallows may also monitor the behavior of distant neighbors who depart from their nests in direct flight (Brown 1986), following these distant neighbors to food sources. As colony size increases, so does the number of distant neighbors for any given individual, and, as a result, the potential foraging information that is available to an individual may increase. In huge colonies of 2000 nests or larger, individuals may never need to wait for a close neighbor to return with food to gain information; in colonies of this size foraging individuals that can be joined are departing continuously (Fig. 1). Not having to wait for information from close neighbors probably saves individuals in large colonies time that can be spent gathering food.

Individuals in large colonies may not have to wait as long for food to be discovered. Food sources are probably discovered faster and more continuously near large Cliff Swallow colonies by virtue of increased numbers of foragers patrolling the foraging grounds. How food sources are discovered by Cliff Swallows, and by which individuals, is still not clear, but large colonies seem to track the locations of food more continuously

than do small colonies, and at any one time probably several food sources are known near large colonies. Continuous tracking of the Cliff Swallow's highly ephemeral food source (Brown 1985) may account for enhanced foraging efficiency of individuals in large colonies. In small colonies food sources are presumably not located as rapidly, and colony residents there must spend more time either searching for food sources themselves or waiting for sources to be discovered by one of the other (few) colony residents.

The absence of a relationship between feeding rates and brood size or nestling age suggests that parental Cliff Swallows continually forage and gather food for their nestlings to the maximum extent possible. Such a pattern is unusual for birds in general and swallows in particular (Moreau 1947, Skutch 1976, Hails and Bryant 1979, Welty 1982, O'Connor 1984). Any increase in Cliff Swallow foraging efficiency, therefore, might represent an appreciable evolutionary advantage in either increased nestling growth or in continued maintenance of adult physical condition, or both. That is, if all individuals regardless of colony size are continually foraging to capacity, then the increased efficiency in a large colony could represent a real net advantage and one that could not theoretically be realized by individuals in small colonies who might just "work harder."

Although my results (Tables 4 and 5) suggest that characteristics of local food resources near colonies probably are not responsible for differences in individuals' foraging efficiencies between sites, there probably are situations where local food resources influence Cliff Swallow colony formation and size. Very large colonies may occur only in areas with certain resource characteristics. For instance, the largest colony size observed in this study was ≈ 3000 nests. Three such colonies were found, one in 1983, 1984, and 1985, respectively. All occurred at the same bridge site, which, prior to 1983, had supported only a few hundred pairs. Unusually heavy spring runoff into the North Platte River, coupled with heavy discharges of water from upstream reservoirs beginning in 1983, raised the river's water level considerably, and in these years the river flooded and created an extensive marsh near the site of the 3000-nest colony. Local food resources in the area were probably much greater than normal in these years. Possibly only an area such as this could have supported 6000 individual Cliff Swallows and their offspring. There was no evidence, however, that any of the other colonies in the study area were located in unusual or exceptional areas. A colony reduction experiment employing even larger colonies (e.g., ≥ 1000 nests) than the ones we used (Table 1) would be useful in further investigating the effects of local resources, but destroying several hundred to a thousand or more Cliff Swallow nests would be impractical and unethical. Although local resource characteristics may determine Cliff Swallow colony sizes only near the extreme upper

limit of the size range, the effects of local food abundance on colony sizes in other colonial animals should be examined.

Some social species feeding in groups improve their foraging efficiency by increasing group vigilance against predators (reviewed by Bertram 1978, Pulliam and Caraco 1984). A possible alternative interpretation of increased waiting intervals in small Cliff Swallow colonies is that individuals increase their scanning for predators when fewer conspecifics are present. Although still an advantage of group living, if individuals improved their foraging efficiencies simply by reducing time spent alert, enhanced food delivery rates and amounts and enhanced nestling growth rates might result from decreased individual vigilance and not from increased opportunities to transfer foraging information.

For three reasons vigilance effects are probably unlikely to be responsible for enhanced foraging efficiency in Cliff Swallow colonies, although vigilance effects are impossible to rule out entirely. First, I have documented that Cliff Swallow colonies are information centers (Brown 1986). If individuals waited near nests to scan for predators, one would expect both successful and unsuccessful individuals to wait and then try to follow others away from the colony (that is, to try not to be the first one to leave). Since successful individuals rarely followed others (Brown 1986) but instead tended to leave their nests soon after feeding their nestlings to return to a foraging site, group foraging is probably not an antipredator behavior. Second, prey capture rates for Cliff Swallows feeding near the center vs. the edge of a foraging flock did not differ (Brown 1985). Thus, these flocks do not appear to function against predators (see Milinski 1977, Jennings and Evans 1980, Inglis and Lazarus 1981). Third, no aerial predators known to be capable of preying on adult Cliff Swallows in foraging flocks occurred in southwestern Nebraska, nor have any such predators been reported from other areas of the bird's range. American Kestrels (*Falco sparverius*) were the only predators present that were potentially able to capture adult swallows away from their nests, but kestrels were seen to capture only recently fledged Cliff Swallows and never showed apparent interest in adult swallows that were foraging.

Discovering that individuals' foraging efficiencies are enhanced in large Cliff Swallow colonies suggests that competition for food probably does not increase with colony size for this species, at least in Nebraska. Competition for food is a potential cost of coloniality in general, and, though generally not directly addressed empirically, evidence suggests that this cost may be important for some birds, especially seabirds (Wittenberger and Hunt 1985, and references therein). The Cliff Swallow's aerial insect food resource probably renews itself sufficiently often that resource depression seldom occurs despite simultaneous utilization by hundreds of individuals in large colonies. Alternative-

ly, resources might be depressed with increasing utilization, but foraging efficiency through information transfer could be sufficiently great to compensate for any resource depression. There are no good data presently to distinguish between these alternative hypotheses. In another colonial swallow, the Bank Swallow (*Riparia riparia*), Hoogland and Sherman (1976) concluded that competition among members of colonies increased in times of poor weather when insect resources were depressed by climatic conditions. However, the frequency of such events and their resulting selective importance are not known for either Bank or Cliff swallows, although poor weather seldom occurs for a long period of time in Nebraska while Cliff Swallows are feeding nestlings.

Nestling growth rates in Cliff Swallows reflect evolutionary trade-offs between the benefits of enhanced foraging efficiency described in this paper and the costs of ectoparasitism documented elsewhere (Brown and Brown 1986). In the presence of ectoparasites, birds in large colonies experience no net advantage in nestling growth rates (Fig. 3b). The incremental gain in nestling body mass in large colonies attributed to enhanced foraging efficiency in the absence of ectoparasites (Fig. 3a, Table 3) is apparently enough to balance the costs of ectoparasitism in colonies exposed to natural levels of swallow bugs. This trade-off may be partly responsible for the diversity in Cliff Swallow colony sizes seen in Nebraska, although other selective forces, some still not understood, also shape the evolution of coloniality in this species (Brown 1985).

Adult Cliff Swallows in large colonies are heavier than adults in small colonies by the end of the nesting season (Fig. 4). This effect is expressed in colonies exposed to natural levels of ectoparasites. The evolutionary implications of increased body mass for adults in large colonies could be important in colony size selection by individuals, especially since individuals selecting a colony of ≈ 2000 nests are likely to maintain body mass during the nesting season (Fig. 4). Many passerine birds lose moderate to large percentages of their pre-breeding body mass during the nesting season (e.g., Ricklefs 1974; see Nur 1984a), and the results reported here for Cliff Swallows are among the first examples that do not fit this pattern. Why some (but not all) adult Cliff Swallows settle in large colonies and presumably benefit from enhanced body mass, is unknown. Beyond ectoparasitism, other costs of coloniality may absorb the apparent evolutionary advantage of enhanced adult body mass in large colonies. Future work is needed to reveal possible relationships between pre-breeding adult body condition, reproductive success the preceding year, adult survivorship, colony size selection the preceding year, and colony size selection during the current year.

In general, empirical studies of "optimal" foraging efficiencies in animals have not linked these efficiencies to reproductive success and subsequent survivorship

(fitness) (e.g., see Kamil and Sargent 1981). The degree to which foraging enhancement in Cliff Swallows described here is reflected in individual fitness is still under investigation (C. R. Brown, *personal observations*). Preliminary results show clearly that heavier Cliff Swallow nestlings are more likely to survive (Brown and Brown 1986). Nestling body mass appears positively correlated with survivorship in some other passerines as well (Perrins 1965, Garnett 1981, Drent 1984, Nur 1984b). For adult Cliff Swallows, it seems likely that heavier individuals at the end of the nesting season would be more likely to survive the fall migration and return to breed again, than Cliff Swallows of low body mass.

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