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ECTOPARASITISM AS A COST OF COLONIALITY IN CLIFF SWALLOWS (*HIRUNDO PYRRHONOTA*)¹

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Abstract. Colonially nesting Cliff Swallows (Passeriformes: *Hirundo pyrrhonota*) in southwestern Nebraska, USA, are commonly parasitized by hematophagous swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*) and fleas (Siphonaptera: Ceratophyllidae: *Ceratophyllus celsus*). We examined to what degree these ectoparasites represent a cost of coloniality for Cliff Swallows. The number of swallow bugs per nest increased significantly with Cliff Swallow colony size. Body mass of nestling swallows at 10 d of age declined significantly as the number of bugs per nestling increased. By fumigating half of the nests in some colonies, killing the bugs, and leaving half of the nests as nonfumigated controls, we showed that swallow bugs lower nestling body mass and nestling survivorship in large Cliff Swallow colonies but not in small ones. Bugs cost nestlings, on average, up to 3.4 g in body mass, and reduced survivorship by up to 50%. Parasitism by fleas showed no consistent relationship with colony size during the nestling period but increased significantly with colony size early in the season, when birds were first arriving in the study area. Fleas did not affect nestling body mass or survivorship and thus, unlike swallow bugs, are probably not important costs of coloniality to Cliff Swallows. Field observations and nest fumigation experiments showed that Cliff Swallows apparently assess which nests are heavily infested with swallow bugs early each spring and select parasite-free nests, leading sometimes to alternate-year colony site usage. Cliff Swallows were more likely to construct new nests (rather than reusing old ones) in large colonies than in small colonies, probably in response to heavier infestations of ectoparasites in the existing nests of large colonies.

Key words: *Ceratophyllidae*; *Ceratophyllus celsus*; *Cimicidae*; *Cliff Swallow*; *coloniality*; *ectoparasitism*; *Hirundinidae*; *Hirundo pyrrhonota*; *mortality*; *Nebraska*; *Oeciacus vicarius*; *reproduction*; *social behavior*.

INTRODUCTION

All social species of animals experience both costs and benefits of living in groups. One such cost is increased transmission of ectoparasites and disease, which is probably a universal hazard to all group-living animals (Alexander 1971, 1974). In colonies, where physical proximity and contact among different individuals are increased, an individual's chances of encountering ectoparasites or pathogens introduced by other group members are increased. Grouped individuals also create greater densities of hosts (a greater "target area") for ectoparasites. Yet, surprisingly, few systematic investigations have related incidence of ectoparasitism or disease transmission to group size. The best studies to date, those of Hoogland and Sherman (1976), Freeland (1979), Hoogland (1979), and W. Shields (*personal communication*), have indeed demonstrated positive correlations between extent of parasitism per individual and colony size. Other, less systematic studies have shown that ectoparasite infestations sometimes have severe effects on colonial birds (e.g., Burgerjon 1964, Chapman 1973, Feare 1976, King et al. 1977, Duffy 1983). Disease transmission as a function of group size has not been empirically studied for any animal, although some reports suggest that outbreaks of disease

are most pronounced in dense concentrations of individuals (Aldous 1941, Dane 1948, Petrides and Bryant 1951, Vermeer 1969, Wobester et al. 1979).

Understanding the dynamics of ectoparasitism and disease transmission is especially critical in understanding the evolution of animal sociality. Even for species in which ectoparasitism has been examined, the severity and regularity of ectoparasitism and its ultimate effect on the structuring and on the evolution of social spacing, are poorly (if at all) known (Wittenberger and Hunt 1985). The goal of this study was to examine to what degree ectoparasitism represents a cost of coloniality to Cliff Swallows (*Hirundo pyrrhonota*). Cliff Swallows are among the most highly colonial landbirds in North America, and are associated with ectoparasites throughout their range. Our study focused on parasitism of Cliff Swallows by a cimicid, the swallow bug (*Oeciacus vicarius*), and a ceratophyllid bird flea (*Ceratophyllus celsus*). For ectoparasitism to represent an important cost of coloniality, it must increase with group size and cause a reduction in fitness of birds in large groups relative to those in smaller groups. Previous studies (Hoogland and Sherman 1976, Hoogland 1979) have suggested that ectoparasitism reduces fitness of parasitized individuals, but direct effects on fitness were not demonstrated. In this paper we quantify the ectoparasites' effects on Cliff Swallows and describe the birds' responses to them. We hope eventually to understand the role of ectoparasitism in the evolution of coloniality in Cliff Swallows.

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STUDY ANIMALS AND STUDY SITE

Cliff Swallows

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). East of the Great Plains, Cliff Swallows are distributed patchily and seldom occur in large numbers, partly in response to usurpation of their nests by House Sparrows (*Passer domesticus*) (e.g., Bent 1942, Samuel 1969). Cliff Swallows 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, which extends from southern Brazil to Argentina and Chile (A.O.U. 1983). The birds build gourd-shaped nests out of mud pellets, and the cantaloupe-sized nests are attached under 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 are aerial insectivores and feed exclusively on insects caught in flight. 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 (Emlen 1941, 1954; C. Brown, *personal observation*). The birds are highly social in all of their activities, feeding, preening, mud-gathering, and loafing in large groups (Emlen 1952, Brown 1985). Nesting within each colony is highly synchronous (Emlen 1952, Myres 1957, Brown 1985), and the species is usually single-brooded. The Cliff Swallow's general biology has been well studied, primarily in Wyoming and California (Emlen 1941, 1952, 1954, Mayhew 1958, Withers 1977), but also in West Virginia and Virginia (Samuel 1971, Grant and Quay 1977).

Swallow bugs

The swallow bug has apparently had a long evolutionary history of association with the Cliff Swallow, and this ectoparasite is found almost exclusively on this bird (Myers 1928, Usinger 1966). Swallow bugs are iteroparous, and nymphs exhibit a lengthy maturation time (Loye and Hopla 1983, Loye 1985). They mate before overwintering, and females may lay eggs as soon as they feed the following spring, without re-mating. Except for a period of dispersal early in the spring, most bugs remain permanently in swallow nests or in crevices of the surrounding nest substrate, and the Cliff Swallow nest itself serves as the focal point for bug-swallow interactions. In many areas annual colony site usage by Cliff Swallows is erratic and the bugs are consequently adapted to an ephemeral host

(food) resource. Adult bugs can perhaps survive in unused swallow nests for up to 3 yr without feeding, since individuals have been found alive in colonies unused by Cliff Swallows for that length of time (Smith and Eads 1978, Loye 1985). Swallow bugs feed at night on the blood of nestling and adult Cliff Swallows, retreating to crevices of the nest and substrate during daylight hours. Bug reproduction is closely synchronized with occupancy of colonies by Cliff Swallows (Loye and Hopla 1983). Bugs disperse each spring by clinging to the bases of the swallows' feathers (Loye 1985), and can be quickly introduced into newly built swallow nests (Foster and Olkowski 1968).

Fleas

The bird flea *Ceratophyllus celsus* is one of several species of ceratophyllid fleas that parasitize Cliff Swallows (Hubbard 1947; C. Hopla, *personal communication*). *C. celsus* is commonly associated with Cliff Swallows and Bank Swallows (*Riparia riparia*) in a patchy (and incompletely known) distribution extending from Texas and New Mexico (Eads 1956, Wheeler et al. 1970; C. Hopla, *personal communication*) northward to British Columbia and Alaska (Hubbard 1947, Haas and Wilson 1979). This flea has probably been associated with Cliff Swallows for at least 2570 yr (Nelson 1972). The life history and dispersal patterns of *C. celsus* are poorly understood, but are the focus of a current investigation (C. Hopla, *personal communication*). These fleas readily disperse from swallow nests by clustering at the entrances and hopping on passing adult Cliff Swallows early in the spring (C. Hopla, *personal communication*). Studies of other species of fleas also suggest that they are most commonly encountered on their avian hosts at the start of the nesting season before nest building (e.g., Fowler et al. 1983). Larvae of *C. celsus* feed on detritus in the nest while overwintering, while adult fleas travel and feed on the blood of adult swallows (and possibly also feed on the blood of nestlings). Fleas, unlike swallow bugs, may thus be more important ectoparasites to adult Cliff Swallows than to nestlings. Fleas cannot survive long periods of nest abandonment by swallows, and mortality is nearly 100% for fleas remaining in colonies that are unused the following year (Hopla and Loye 1983). Hopla and Loye (1983) summarize other known features of the general biology of *C. celsus*.

Study site

This study, part of continuing long-term research on the social behavior of Cliff Swallows, was done in southwestern Nebraska, USA, in the vicinity of the Cedar Point Biological Station, from May to August, 1982–1985. 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. These birds probably occurred in southwestern Nebraska before the appearance of artificial structures,

however, nesting on bluffs and outcrops along the North Platte River and also on cliffs in other parts of the state (Nichols, cited in Pearson 1917). 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 1982–1985, we studied 167 Cliff Swallow colonies totalling 53 308 nests in Keith, Garden, and Lincoln Counties (Brown 1985). Colony size ranged from 1 to ≈ 3000 nests ($\bar{X} = 319.2$, $SD = 522.0$). The most common colony size was ≈ 350 nests.

METHODS

General procedures and definitions

Study colonies were named and, where possible, all nests were numbered and 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 base of a cliff site or into a culvert 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). Colored flags attached to the nails or walls facilitated identification of these nests at a distance. All nests were checked each day or every 2–3 d until hatching started, at which time we began checking them 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 in any appreciable way, 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 energetic or time demands on the birds.

Once all eggs of a Cliff Swallow clutch hatched, we did not disturb that nest again until the nestlings were 10 d old, at which time we recorded the body masses of the nestlings (Hoogland and Sherman 1976) with a 50-g Pesola scale and examined them for ectoparasites. Day 10 was selected because that is the time of maximum gain in nestling body mass for Cliff Swallows (Stoner 1945), and we wanted a measure of the degree to which nestlings were stressed by ectoparasites. All swallow bugs and fleas that were present on each nestling at 10 d of age were counted. Nestlings of that age were still sparsely feathered, and bugs and fleas could not hide in feathers to escape detection. Since data from nestlings within the same nest were not statistically independent, we averaged body mass and bug and flea

counts for all nestlings within each nest and examined the respective mean values per nest. All nestlings were banded 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 the nestlings, but we rebuilt the nests' necks with mud, and the swallows added to our repair jobs with mud of their own.

"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, we estimated smaller colony sizes later in the season for those colonies. 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, at least 25 m separated them from the nearest group of nests, and 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 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, if ever, interacted with each other.

Statistical analyses were performed on the Princeton University IBM 3081 computer, using the Statistical Package for the Social Sciences (Nie et al. 1975). All statistical tests were two-tailed. Since data were not normally distributed in most cases, nonparametric statistical tests were used (Siegel 1956). Significance was set at $P = .050$.

Measuring nest densities and positions

We calculated nest density of each Cliff Swallow colony by first measuring the total available substrate that appeared suitable for nest attachment. We conservatively considered the active nests closest to the colony edges to indicate the limits of suitable substrate, and therefore defined the distance between opposite edge-most nests to be the extent of suitable habitat. The number of nests located on this expanse of substrate was determined, and we expressed density as nests per metre. Because most of our colonies were roughly linear in shape, i.e., single rows of nests with little vertical stacking, "nests per metre" seemed to be the most realistic measure of density for virtually all colonies.

The positions of all nests in each colony were mapped at the end of the nesting season. Relative nest locations were drawn on paper, and overlapping series of pho-

tographs at some colonies provided further documentation of nest positions. Distances between all active nests were measured (in centimetres) in the field. Since colonies were usually linear in shape, it was easy to designate a centermost nest, one with an equal number of neighbors on either side. For the few colonies that were less linear in shape and more "honeycombed," the nest with an equal number of nests on all respective sides was considered the centermost nest (even though it may have been located far from the geometrical center of the available substrate). Each nest's linear distance from the centermost nest in its colony was used as a measure of whether it was located near the center or the edge of the colony.

Categorizing nests as new or old

We examined the effect of colony size on the birds' tendencies to construct new nests or reuse old ones. The progress of all Cliff Swallow nests started in our study colonies was charted every day or every other day. We estimated the extant proportion of each nest, using categories such as "bottom only," "one-fourth to one-half present," "neck incomplete," or "complete." Any nest that was completely new (i.e., no previous nest remnant had been present at that location on the substrate) in a given year, or any nest built from an existing remnant that upon becoming active (known by deposition of fresh mud) was one-half or less complete, was considered a new nest. Existing nests that were more than one-half complete when becoming active were considered old nests. A nest was not included in this analysis if we did not know its status at the time it became active.

Sampling swallow bugs

We examined the relationship between extent of swallow bug infestation and Cliff Swallow colony size in two ways. One way was to record the number of bugs present on each nestling swallow at 10 d of age in colonies of different sizes (see General Procedures and Definitions). A second way was to collect recently vacated Cliff Swallow nests and count all swallow bugs present in each nest. Collection of nests was necessary to insure that the bugs hiding in the nests or in crevices of the adjacent substrate during daylight hours were represented in our samples. In 1983 and 1984, we collected 260 Cliff Swallow nests from 19 colonies in July and August after nestlings had fledged, and counted all swallow bugs present in each nest. Each nest was collected 2–7 d after the nestlings present there had fledged, which was also the time of year when bug infestations were greatest (Brown 1985, Loye 1985). Only nests that had earlier contained nestlings were sampled. Nests, kept as intact as possible, were placed in plastic bags, returned to the laboratory, and in most cases left bagged for 1–4 d before bug counting commenced. Bugs were counted by placing each nest in a pan and sifting through the nest materials by hand, breaking up chunks of dried

mud to expose bugs. Each nest took from 15 to 60 min to count. There was no obvious bug mortality resulting from bagging. All collected nests were completely removed from a colony substrate, and no nest was used if large portions of it were lost. At many nests, removal exposed dense aggregations of bugs that had wedged themselves between the nest and the surface of the substrate. Many of these bugs were not clinging to any nest material and hence were not bagged; thus, at the time of collection we also estimated the number of bugs left in each nest's "scar" upon the substrate. These estimates were included in each nest's total bug count.

Fumigation procedures

In 1984 swallow bugs were experimentally removed from Cliff Swallow nests by fumigation. We used a short-lived fumigant, Dibrom, which breaks down rapidly both with water and when exposed to light. This fumigant had been used successfully without harming avian hosts (Purple Martins [*Progne subis*] and Cliff Swallows) by Moss and Camin (1970) and Chapman (1973), and we never detected it having any adverse effects on Cliff Swallows. The fumigant was diluted 1 part to 170 parts water (by volume) (Chapman 1973) and applied as a fine mist to the outside of swallow nests and the surrounding substrate. Nests were fumigated daily or every other day, beginning as soon as birds established ownership of nests and continuing until nestlings fledged or approached fledging. Colonies were arbitrarily divided in half, and the "control" half of each colony was not fumigated. A sticky insect barrier known as Tree Tanglefoot was applied to the substrate between the halves of each colony to prevent bugs from leaving the fumigated nests and entering the nonfumigated nests. In addition, all fumigated nests were surrounded by Tanglefoot applied to the substrate to prevent new bugs from immigrating into the fumigated nests over the course of the season. Average clutch size and brood size at hatching did not significantly differ between fumigated and nonfumigated nests (Table 1), suggesting that any subsequent differences observed in either nestling body mass or survivorship could be attributed to the fumigant treatment. The fumigant was highly effective against swallow bugs; no bug was recorded on any nestling hatched in a fumigated nest ($N = 558$ nestlings). At day 10, body mass of nestlings and nestling survivorship were recorded, and ectoparasites were counted. Since there appeared to be differences in levels of ectoparasite infestation between bridge and culvert colonies (and possibly between cliff and culvert colonies), only culvert colonies were used for the fumigation experiment.

Sampling fleas

Owing to the poorly understood life history of *C. celsus*, we were unsure when and how to sample fleas to best examine the effect of colony size on their populations. We thus sampled fleas in two ways at two

TABLE 1. Clutch size and brood size of Cliff Swallows in fumigated (F) and nonfumigated (NF) nests in six Nebraska colonies, 1984.

Colony size (no. active nests)		Clutch size†				Brood size‖			
		\bar{X}	SE	N‡	P§	\bar{X}	SE	N‡	P§
<10	F	3.5	0.3	8		3.0	0.5	7	
	NF	3.3	0.4	11	.60	3.0	0.7	4	.92
43	F	3.7	0.1	12		3.2	0.2	21	
	NF	3.4	0.2	11	.38	3.4	0.2	19	.57
56	F	3.2	0.2	33		2.9	0.2	16	
	NF	3.4	0.2	24	.32	3.1	0.1	7	.59
75	F	3.7	0.2	18		3.1	0.2	16	
	NF	3.6	0.2	17	.81	2.9	0.2	15	.64
125	F	3.0	0.1	41		2.7	0.1	33	
	NF	2.9	0.1	86	.31	2.6	0.1	40	.46
345	F	3.8	0.1	122		3.4	0.1	86	
	NF	3.9	0.0	223	.41	3.3	0.1	69	.48

† Measured as the maximum number of eggs ever appearing in a nest.

‡ Sample size (number of nests). In some cases, the total sample size (F plus NF nests) was greater than colony size because re-nestings (by birds that had lost their first clutch) were included in the sample size but did not affect colony size (for 56- and 125-nest colonies), or because data from several colonies with <10 nests were pooled.

§ From Mann-Whitney *U* tests comparing F and NF nests.

‖ Measured as the number of eggs that hatched in a nest.

different times: by counting fleas on nestlings 10 d after hatching, and by sampling fleas that clustered at nest entrances early in the nesting season before most Cliff Swallows had returned to the study area.

Flea sampling at nest entrances was done using methodology adapted by Hopla and Loye (1983) from Humphries (1969). Samples were taken by placing a black card, coated with honey, ≈ 5 cm from each nest's tube-like entrance. The black card mimicked a bird's blocking the entryway and stimulated the negatively phototactic fleas (clustered at the nest entrance) to jump onto the card, where they were trapped by the honey and could be counted. A card was held in front of each nest for 20 s; this time was sufficient for large numbers of fleas to leap onto the card. These samples had to be taken at colonies immediately prior to the Cliff Swallows' arrival. If nests were sampled far in advance of the birds' arrival, fleas were presumably still in the recesses of the nests and had not clustered at the entrances. If the samples were taken any time after the birds' initial visit to a colony, few fleas appeared on the cards, probably because the fleas had already leaped onto the birds. Clustering of fleas at nest entrances is synchronized closely with the birds' arrival in Oklahoma (Hopla and Loye 1983) and in our study area (C. Brown and M. Brown, *personal observation*), the only places where fleas have been card-sampled to date. Card-sampling was done in 1983 at 343 nests in six colonies on two dates just prior to and during arrival of Cliff Swallows in the study area.

RESULTS

Ectoparasitism by swallow bugs

Relationship to colony size and density.—Since swallow bugs are transported between colonies by Cliff Swallows (Foster and Olkowski 1968, Loye 1985), the probability of swallow bug introduction to a site theoretically increases with the number of birds colonizing the site. Also, the denser colonies theoretically facilitate the spread of bugs, once introduced, to other nests. We therefore predicted that large and dense Cliff Swallow colonies would have greater infestations of swallow bugs than would small and spread-out colonies.

The number of swallow bugs per nestling increased significantly with colony size in 1982 and 1983 (Fig. 1a), and in 1984 (Fig. 1b). Heavier overall levels of bug infestation occurred for unknown reasons in 1984. The number of swallow bugs per nest also increased significantly with colony size, both on bridges (Fig. 2a) and in culverts (Fig. 2b). (Counts from colonies located on bridges and those in highway culverts are presented

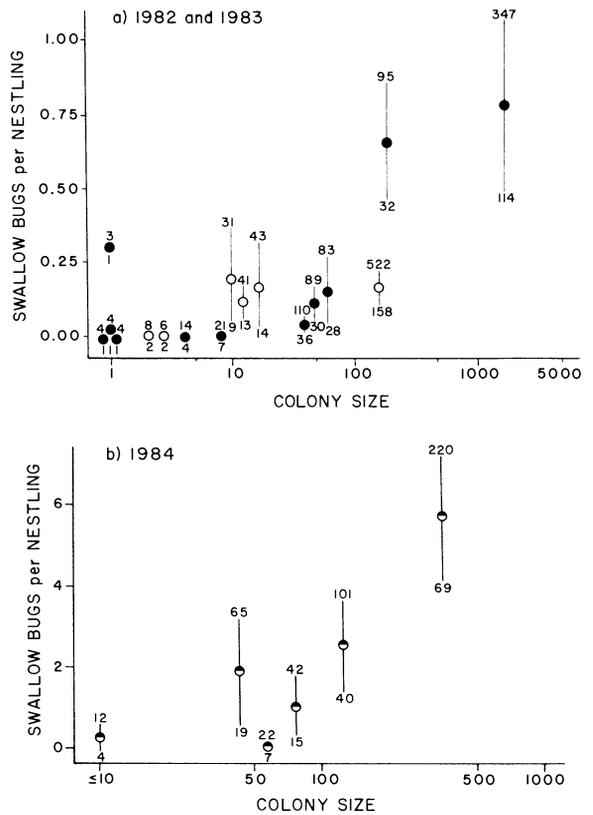


FIG. 1. Level of swallow bug infestation of nestling Cliff Swallows at 10 d of age versus colony size (number of active nests) in (a) 1982 (●) and 1983 (○) and (b) 1984. Means ± 1 SE shown. Note different ordinate scales in (a) and (b). Total number of nestlings and nests sampled for each colony size shown above and below error bars, respectively. The number of swallow bugs per nestling increased significantly with colony size in 1982 and 1983 ($r_s = 0.11$, $P = .008$) and in 1984 ($r_s = 0.37$, $P < .001$).

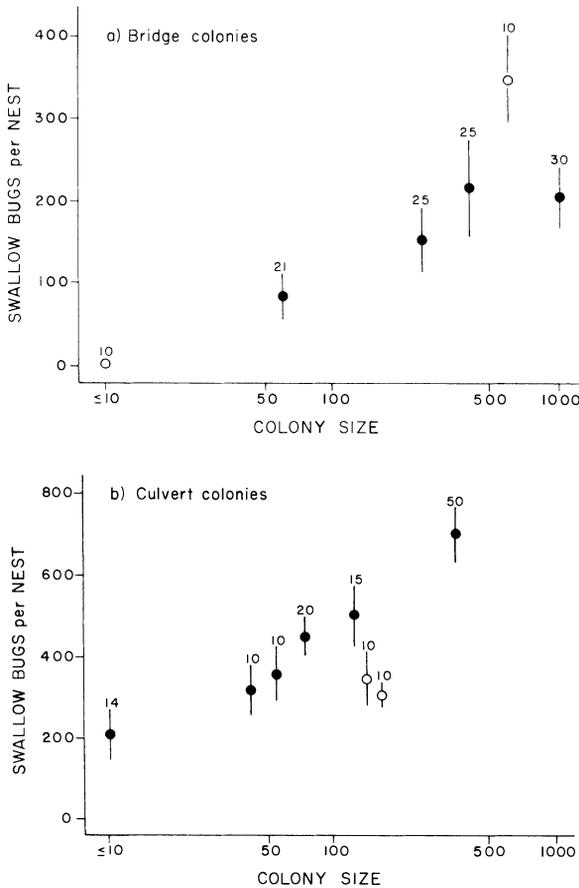


FIG. 2. Level of swallow bug infestation in collected Cliff Swallow nests versus colony size (number of active nests) for colonies located (a) on bridges and (b) in highway culverts in 1983 (○) and 1984 (●). Means \pm 1 SE shown. Note different ordinate scales in (a) and (b). Total number of nests sampled for each colony size shown above error bars. The number of bugs per nest increased significantly with colony size for bridge colonies ($r_s = 0.51, P < .001$) and for culvert colonies ($r_s = 0.45, P < .001$). Data from all culvert colonies of < 10 nests were pooled.

separately in Fig. 2 because colonies in culverts had noticeably heavier infestations of bugs than ones located on the more exposed highway bridges and overpasses. Some nests from culvert colonies contained up to 2500 bugs each.)

The number of swallow bugs per nest increased significantly with colony density (Fig. 3). Since bridges in general tended to support less dense colonies (Fig. 3), this fact may account for the difference in infestation levels between bridge and culvert colonies (Fig. 2).

One potential confounding variable for the results in Figs. 1–2 is time of year. If large (or small) colonies tended to start earlier or later than other colonies, our samples might reflect the phenology of swallow bugs rather than simple colony size effects. The number of bugs per nestling increased significantly as the nesting season advanced (based on the date on which the counts

were taken) ($r_s = 0.34, P < .001, N = 2194$ nestlings, 707 nests). This result means that bugs could have been more plentiful in large colonies simply due to later starts by large colonies than by small ones. Yet in separate analyses for each year, and for all years combined, bug infestations increased significantly with colony size independent of date (combined years, $F = 19.6, df = 3, 549, P < .001$, multiple regression). Furthermore, large colonies in our study area in general tended to start earlier than small colonies, suggesting that the relationship between extent of swallow bug infestation and colony size was real.

Effects on nestling body mass and survivorship.—To learn whether swallow bugs reduce Cliff Swallow fitness, we initially examined whether average nestling body mass was related to extent of ectoparasitism. Body mass per nestling declined significantly as swallow bugs per nestling increased (Fig. 4).

These data suggest that increased ectoparasite loads caused slower nestling growth rates and, since bugs are more numerous in large colonies (Figs. 1–2), indirectly suggest that fitness of birds in large colonies is depressed. However, to establish directly that swallow bugs reduce fitness of birds in large colonies and thus constitute a real cost of group living, we analyzed results of the fumigation experiment. In this experiment we removed swallow bugs and their presumed effects in colonies of different sizes by fumigating nests and then compared nestling body mass and nestling survivorship between fumigated and nonfumigated nests. We predicted that, if bugs are an important cost of coloniality for Cliff Swallows, differences between fumigated and nonfumigated nests should be large in large colonies and small in small colonies. We thus examined directly the relative effect of bugs in different-sized colonies.

Average nestling body mass was significantly greater

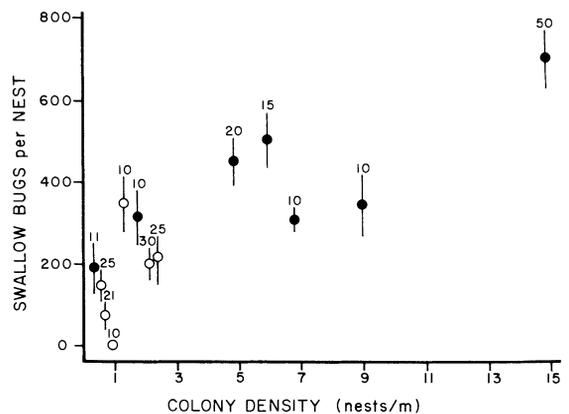


FIG. 3. Level of swallow bug infestation in collected Cliff Swallow nests versus colony density for colonies located on bridges (○) and culverts (●) in 1983 and 1984. Means \pm 1 SE shown. Total number of nests sampled for each colony density shown above error bars. The number of bugs per nest increased significantly with colony density ($r_s = 0.63, P < .001$).

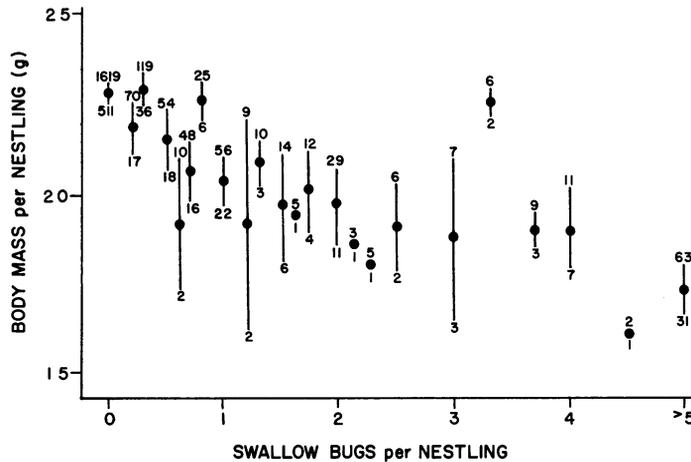


FIG. 4. Body mass of nestling Cliff Swallows at 10 d of age versus level of swallow bug infestation. Means \pm 1 SE shown. Total number of nestlings and nests sampled for each degree of swallow bug parasitism shown above and below error bars, respectively. Nestling body mass declined significantly as the number of swallow bugs per nestling increased ($r_s = -0.39$, $P < .001$). No nestlings from fumigated nests were included in this analysis.

in fumigated nests than in nonfumigated nests for the four largest colonies (Table 2), and the same trend, though the differences were not significant, held for the two smaller colonies. The relative difference between average nestling body mass in fumigated versus nonfumigated nests increased consistently with colony size for the four largest colonies, from a difference of 2.5 g in the 56-nest colony to one of 3.4 g in the 345-nest colony (Table 2). These data thus suggest that hematophagous swallow bugs may cost nestling Cliff Swal-

lows, on average, up to 3.4 g in body mass, an appreciable loss since mean nestling body mass at 10 d is 22.2 g ($N = 2194$ birds).

Reductions of several grams in body mass probably led to slower nestling growth rates, and often the effects of swallow bugs were much more severe. Nestlings with five or more bugs on them (and in some nonfumigated nests nestlings had up to 82 bugs) in all cases were so feeble and malnourished that they probably died soon after we examined them (Fig. 5). Parasitism by swallow bugs was reflected in nestling survivorship. In the two largest colonies, where effects of bugs were most pronounced, nestling survivorship to day 10 was significantly greater in the fumigated nests than in the nonfumigated nests (Table 3). Since brood sizes in both classes of nests were similar at hatching (Table 1), mortality during the nestlings' first 10 d attributable to bugs was very high (Table 3).

TABLE 2. Body mass of nestling Cliff Swallows at 10 d of age in fumigated (F) and nonfumigated (NF) nests in six Nebraska colonies, 1984.

Colony size (no. active nests)		Nestling body mass (g)			N^\dagger	P^\ddagger
		\bar{X}	SE			
<10	F	22.9	0.9	7	.19	
	NF	20.3	1.1	4		
43	F	23.9	0.5	21	.052	
	NF	22.1	0.8	19		
56	F	24.0	0.5	16	.038*	
	NF	21.5	1.1	7		
75	F	23.8	0.3	16	<.001*	
	NF	21.1	0.5	15		
125	F	24.2	0.3	33	<.001*	
	NF	21.0	0.7	40		
345	F	23.7	0.2	86	<.001*	
	NF	20.3	0.3	69		

† Sample size (number of nests). For the colony size listed as <10 nests, the total sample size (F plus NF nests) is >10 because data from several colonies were pooled.

‡ From Mann-Whitney U tests comparing F and NF nests. Since body masses of nestlings within a nest were not statistically independent, analyses were based on average nestling body mass for each nest. Significant differences indicated by *.

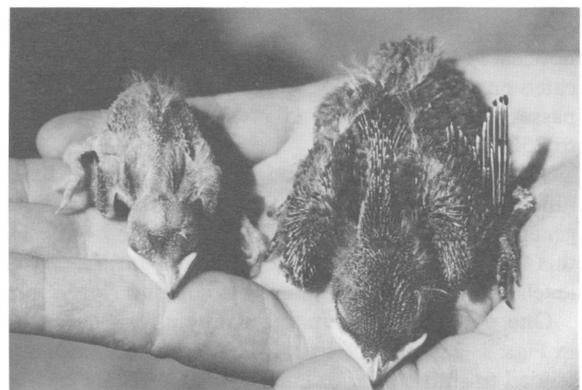


FIG. 5. Typical nestling Cliff Swallow from a nonfumigated nest (left) and from a nest fumigated with an insecticide that kills swallow bugs (right) at a 345-nest colony. Both were 10 d old.

TABLE 3. Number, per nest, of nestling Cliff Swallows surviving to 10 d of age in fumigated (F) and nonfumigated (NF) nests in seven Nebraska colonies, 1984.

Colony size (no. active nests)		Survivors (no. young per nest)		N†	P‡
		\bar{X}	SE		
<10	F	2.3	0.5	9	
	NF	1.1	0.6	11	
30	F	3.9	0.2	11	.17
	NF	3.1	0.1	12	
43	F	2.9	0.3	23	.30
	NF	3.4	0.2	19	
56	F	1.4	0.3	33	.20
	NF	0.9	0.3	24	
75	F	2.7	0.3	18	.66
	NF	2.5	0.3	17	
125	F	2.4	0.1	41	<.001*
	NF	1.4	0.1	86	
345	F	3.1	0.1	96	<.001*
	NF	1.4	0.2	154	

† Sample size (number of nests). In some cases, the total sample size (F plus NF nests) was greater than colony size because re-nestings (by birds that had lost their first clutch) were included in the sample size but did not affect colony size (for 56- and 125-nest colonies), or because data from several colonies with <10 nests were pooled.

‡ From Mann-Whitney *U* tests comparing F and NF nests. Significant differences indicated by *.

These differences in nestling survivorship were further reflected in annual survivorship data. In the course of our research with Cliff Swallows in 1985, we encountered 50 banded individuals hatched the preceding year in the experimental colonies. Of these, the number that had been hatched in fumigated nests (34)

was significantly more than the number hatched in nonfumigated nests (16) ($\chi^2 = 3.94, P = .047$; total banded in fumigated nests = 558 nestlings, total banded in nonfumigated nests = 462 nestlings). These results clearly suggest that annual survivorship was enhanced for parasite-free birds.

Ectoparasitism by fleas

Relationship to colony size.—Since fleas disperse by leaping onto passing Cliff Swallows and traveling on the birds, the probability of flea introduction to a site theoretically increases with the number of Cliff Swallows colonizing that site. We predicted that flea infestation levels would increase with colony size.

The number of fleas per nestling increased significantly with colony size (Fig. 6), but there was extensive variation between and within colonies. The reason for this variation was not clear, so we examined whether time of year influenced levels of flea infestation. Nestlings hatched early in the season had significantly more fleas than ones hatched late in the season ($r_s = -0.06, P = .045, N = 2194$ nestlings, 707 nests). However, both colony size and date, independent of each other, explained significant amounts of the variation in flea counts per nestling ($F = 16.6$ and 11.8 , for colony size and date, respectively, $df = 3, 703, P < .001$ in each case, multiple regression). Based strictly on flea counts from nestlings, there does not appear to be an important effect of colony size on extent of flea infestation, because of the extreme variation between and within colonies (Fig. 6).

When sampling fleas at nests early in the spring, however, we found a dramatic effect of colony size on extent of flea infestation (Fig. 7). Nests in the largest

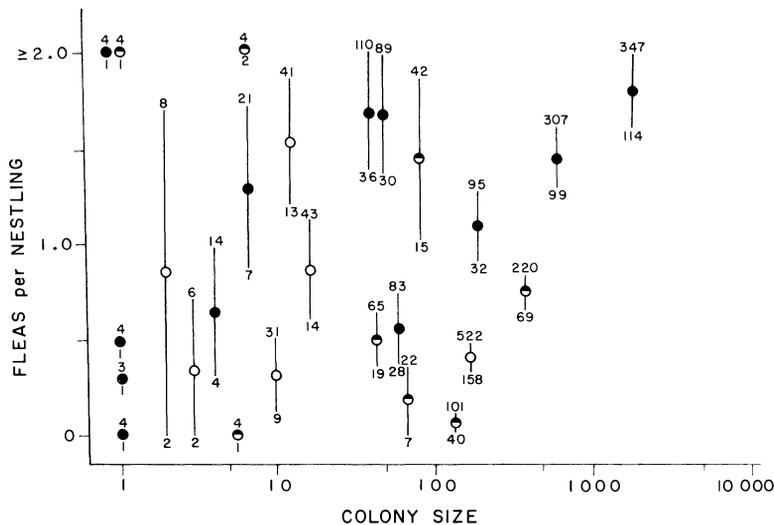


FIG. 6. Level of flea infestation of nestling Cliff Swallows at 10 d of age versus colony size (number of active nests) in 1982 (●), 1983 (○), and 1984 (half-open circles, nonfumigated nests). Means ± 1 SE shown. Total number of nestlings and nests sampled for each colony size shown above and below error bars, respectively. The number of fleas per nestling increased significantly with colony size ($r_s = 0.21, P < .001$). Means for three colonies that exceeded 2.0 fleas per nestling are depicted at 2.0 in order not to compress the scale of the graph.

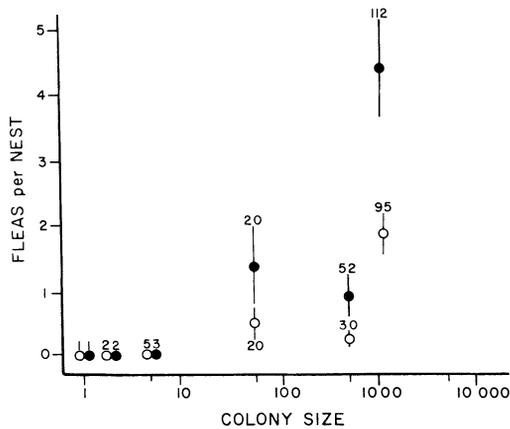


FIG. 7. Level of flea infestation per nest versus Cliff Swallow colony size (number of active nests). Means \pm 1 SE shown. Samples were taken at each colony twice, 9 May (○) and 22 May (●) 1983. The number of fleas per nest increased significantly with colony size on each date (9 May: $r_s = 0.48$, $P < .001$; 22 May: $r_s = 0.35$, $P < .001$).

colony had up to 39 fleas each, while no fleas were found in nests in the smallest colonies. The total number of fleas in nests tended to increase as more birds arrived in the study area, but the relative difference between colonies of different sizes remained similar (Fig. 7). Clearly, early in the spring nests in large Cliff Swallow colonies harbored considerably more fleas than did nests in small colonies, and this effect of colony size was not masked by extensive within- or between-colony variation.

Effects on nestling body mass.—We examined whether fleas affected the body mass of nestling Cliff Swallows and thus (potentially) the birds' fitness. Surprisingly, body mass per nestling increased significantly as the number of fleas per nestling increased (Fig. 8). This suggests that fleas represent little, if any, physiological cost to nestling Cliff Swallows. Perhaps they crawled on nestlings at random and our counts showed increased levels of infestation on heavier nestlings simply because those birds were larger and offered a greater surface area. Since fleas do not depress nestling body mass, they probably do not appreciably lower Cliff Swallow fitness (although we were unable to evaluate their potential effects on adult swallows). We could not investigate flea ectoparasitism experimentally by fumigating nests because apparently Dibrom is ineffective against *C. celsus*. In only one colony did the number of fleas on nestlings in fumigated versus nonfumigated nests differ significantly (see Brown 1985).

Responses of Cliff Swallows to ectoparasites

Assessment of infested nests.—Given the substantial costs of swallow bug parasitism, Cliff Swallows might be expected to exhibit behavior that minimizes these costs. The most effective behavior for avoiding bugs

could be to skip one or more years between use of existing nests or of an entire colony site (Grinnell et al. 1930, Chapman 1973), which would presumably allow time for bug populations there to decrease. This hypothesis implies that Cliff Swallows are able to assess which nests or which colonies are heavily infested with ectoparasites and then to avoid them. We observed patterns in nest site usage within two Nebraska colonies that provide the first empirical support for the notion that these birds are able to accurately assess ectoparasite loads from the previous year before selecting nest sites early in the spring.

In early spring, 1985, substantial numbers of old nests remained, largely intact, in the two largest colonies in which we had fumigated nests in 1984. These colonies we termed the "Garden County" and "Keith County" colonies, based on their locations. As soon as birds arrived in the study area in 1985, the old nests in the sections of these colonies that had been fumigated the preceding year and that were thus parasite-free, were immediately occupied. The nonfumigated nests from the preceding year were completely ignored at the Garden County colony and virtually ignored at the Keith County one, even though fumigated and nonfumigated nests were in some cases separated by < 1 m. Nest occupancy in these sections of the colonies was scored as of 26 May 1985 (Table 4). We maintained the 1984 fumigation scheme in 1985 at the Garden County colony, only fumigating the nests that had been previously fumigated. No Cliff Swallows ever used any of the nonfumigated nests in 1985 at the Garden County colony. However, on 26 May 1985 we began fumigating the entire Keith County colony. Although birds had previously showed virtually no interest in the nonfumigated nests at that colony (Table 4), by 3 June 1985 large numbers of birds were investigating and defending nests in all sections of this colony. By 28 June, 456 additional nests had been constructed or (if already present) had become active. Of those, 174 were in the former (1984) fumigated section and 282 were in the former nonfumigated section.

These experimental results from two colonies indicate that Cliff Swallows do assess relative degree of ectoparasite infestation among nests in colonies early in the year and that parasite-free nests are quickly occupied (Table 4). Since both fleas (Hopla and Loye 1983) and swallow bugs (*C. Brown, personal observation*) cluster in plain sight at the entrances of nests early in the spring, visual assessment by the birds seems likely. Cliff Swallows commonly hover a few centimetres in front of old nests early in the spring immediately upon their arrival in the area, not entering the nests, and it is at that time that assessment of ectoparasites probably occurs.

Abandonment of infested nests.—Our observations also indicated that Cliff Swallows, having chosen a colony site, probably continually assess ectoparasitism within their colonies throughout the nesting season.

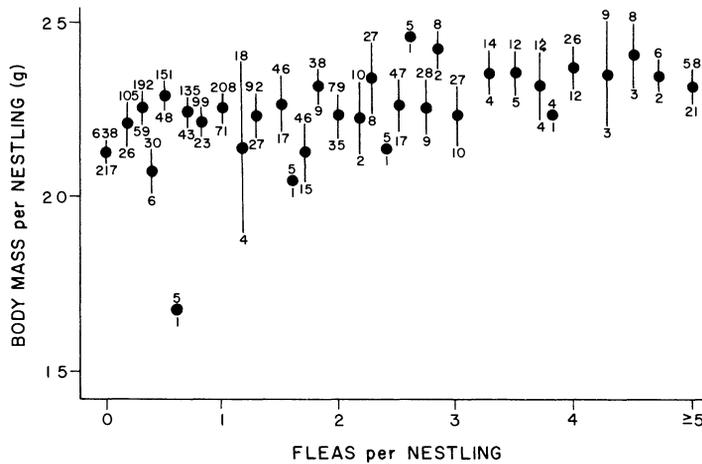


FIG. 8. Body mass of nestling Cliff Swallows at 10 d of age versus level of flea infestation. Means \pm 1 SE shown. Total number of nestlings and nests sampled for each degree of flea parasitism shown above and below error bars, respectively. Nestling body mass increased significantly as the number of fleas per nestling increased ($r_s = 0.20, P < .001$). No nestlings from fumigated nests were included in this analysis.

Mass desertions by late-nesting birds sometimes occurred when bug infestations (which increased as the nesting season progressed) became so severe that successful reproduction by Cliff Swallows was unlikely. In 1982 at a 1600-nest colony and in 1984 at a 2000-nest colony, we observed sudden mass abandonment of nests by Cliff Swallows at the end of the nesting season. Exact figures were not taken, but 100–200 nests containing eggs and nestlings were abandoned at each colony. Some individuals from the 2000-nest colony switched to another site 2 km away and initiated new nests at this much smaller (125-nest) colony a week after the mass desertion. Similarly, mass desertions by late-nesting birds occurred among the nonfumigated nests in a 345-nest colony in 1984; no desertions occurred among the fumigated nests there. These desertions, similar to those reported elsewhere (Foster 1968, C. Hopla and J. Loye, *personal communication*), were clearly a response to ectoparasitism. In the Nebraska colonies affected, bug infestations were tremendous, with hundreds to thousands of bugs present on the outside and inside of all the nests and throughout the adjacent nesting substrate.

Constructing new nests.—Another possible way for birds to avoid ectoparasites is to construct an entirely new nest. Although reuse of Cliff Swallow nests in subsequent years is common in Nebraska, the birds also frequently build new nests, even in colonies where old nests are extant. If levels of bug infestation are high in large colonies but low in small colonies, we predicted that Cliff Swallows should be more likely to construct entirely new nests in large colonies than in small colonies. In small colonies with few bugs, we predicted that birds would be more likely to use old, existing nests.

The percentage of total nests that were constructed anew in a given year increased significantly with colony size ($r_s = 0.83, P < .001, N = 29$ colonies). For the

three colony size classes represented in the fumigation experiment, mean percentages (\pm SE) of nests constructed anew were: $0.0 \pm 0.0\%$ for 13 colonies of 1–10 nests, $52.9 \pm 10.3\%$ for 10 colonies of 11–99 nests, and $57.3 \pm 4.9\%$ for 6 colonies ≥ 100 nests in size. Because nest durability differed between colonies located on exposed bridges or cliff sites versus those in more protected highway culverts, for this analysis we used only culvert colonies (for which we had the greatest sample size). This reduced any substrate-related biases in these results.

Nest position within the colony.—Ectoparasites potentially can be avoided by nesting toward the edges of a colony, where nest densities are reduced. We examined whether ectoparasite infestations varied with nest position within Cliff Swallow colonies. There was

TABLE 4. Nest usage as of 26 May 1985 in sections of two colonies in each of which some nests had been fumigated and some left unfumigated the preceding summer.

	Fumigated	Nonfumigated
Garden County colony		
Old nests present	89	155
Old nests unused	3	155
Old nests used†	86	0
New nests built	4	0
Total active nests	90	0
Keith County colony		
Old nests present	57	94
Old nests unused	18	91
Old nests used†	39	3‡
New nests built	0	0
Total active nests	39	3

† A nest was defined as being used if at least one egg was laid in it.

‡ Two of these nests were immediately adjacent to the line dividing the fumigated and nonfumigated halves of the colony.

a weak but significant inverse correlation between the number of swallow bugs counted on nestlings and a nest's linear distance from the centermost nest (all years combined, $r_s = -0.10$, $P = .004$, $N = 640$ nests). There was a similar, though not significant, relationship between the number of fleas counted on nestlings and a nest's linear distance from the centermost nest (all years combined, $r_s = -0.06$, $P = .079$, $N = 640$ nests). These results indicate that Cliff Swallows nesting toward the edges of colonies might partly escape the heavier infestations of ectoparasites that are found near the centers of colonies. Swallow bugs and fleas probably cluster toward the centers of colonies to maximize their chances of finding an active nest and hence a blood meal.

DISCUSSION

This study demonstrates that parasitism by swallow bugs is a serious cost of coloniality for Cliff Swallows. This cost is expressed as a direct effect on fitness, because the number of these bugs increases with colony size, and infestations clearly reduce nestling body mass and survivorship. Swallow bugs in the larger colonies kill nestling swallows outright and affect even the surviving birds through the reductions in body mass. As suggested by the data on annual survivorship of Cliff Swallows raised in fumigated versus nonfumigated nests and by Perrins' (1965) work with Great Tits (*Parus major*), reductions in body mass could be serious handicaps for nestlings once they fledge, because in passerines nestling body mass probably is positively correlated with postfledging survival.

Host-parasite systems, such as the Cliff Swallow/swallow bug one, with such consistently (and heavily) deleterious effects on the hosts are apparently quite rare (e.g., Marshall 1981). Since swallow bugs are specialized as Cliff Swallow parasites, this system is probably evolutionarily old, and yet, curiously, these tremendously deleterious effects on the hosts have persisted. Deleterious effects are not confined to Nebraska because Chapman (1973), studying Cliff Swallows in Texas, also concluded that hematophagous ectoparasites (including some ticks at his site) reduced nestling body mass and growth and caused nestling mortality. Also, in Oklahoma, the average swallow bug infestation per nest may be at least double what we observed in Nebraska (Loye and Hopla 1983, Loye 1985).

In some areas Cliff Swallows are parasitized by several species of ticks in addition to swallow bugs and fleas (Baerg 1944, Kohls and Ryckman 1962, Chapman 1973, Hopla and Loye 1983). Ticks occur quite rarely in our study area; we encountered only five individuals of *Ornithodoros concanensis* (Acarina: Argasidae) in handling 2194 nestling Cliff Swallows. In other areas, such as west-central Oklahoma, however, ticks may be as numerous as swallow bugs and represent even more of a physiological cost to Cliff Swallows than do bugs (C. Hopla, *personal communication*). The Cliff Swal-

low as a host-resource is evidently under heavy pressure from several kinds of parasites throughout most of its range. Competition within this parasite community cannot automatically be assumed (Price 1980), but would be worth examining since little is known of the interrelationships among the Cliff Swallow parasites. In our study area, there does appear to be a temporal separation in peak infestation levels between fleas and swallow bugs. Fleas are most common early in the season and probably mate and lay eggs before swallow bugs do. Bugs are most common late in the season. This separation was reflected in an inverse correlation between the number of fleas and the number of bugs counted on nestling swallows, fleas being on the early nestlings and bugs on the later ones ($r_s = -0.14$, $P < .001$, $N = 2194$ nestlings, 707 nests). Cliff Swallows are exposed to ectoparasites of one form or another from the time they arrive in North America each spring until they depart.

Ectoparasitism probably affects many aspects of Cliff Swallow biology. Our observations suggest that these birds assess levels of ectoparasite infestation before selecting nest sites in the spring, which means that individual swallows often may visit several different colony sites before selecting one. Irregular annual colony site usage by Cliff Swallows has been reported in Arizona (S. Speich, *personal communication*), in Texas (Chapman 1973, Sikes and Arnold 1984), in Oklahoma (Hopla and Loye 1983), and in Nebraska (Brown 1985). In Oklahoma and Arizona, birds may skip up to five consecutive years between use of a given site, and some sites may be used only once. Our observations clearly suggest that these irregularities in site usage are caused by levels of ectoparasite infestations. Alternate year colony site (or nest) usage could indeed be effective in avoiding bugs. Although some bugs might survive in unused nests for up to 3 yr, appreciable mortality of swallow bugs occurs the first winter after a reproductive bout (Loye 1985). If a colony was unused for a season, by the end of the second winter populations of bugs could be substantially reduced.

Ectoparasites may also affect Cliff Swallows' tendencies to reuse old nests or build new ones. Building a new nest in a large colony may provide a temporary respite from the swallow bugs that still survive in old nests at the beginning of the nesting season. However, construction of new nests in large colonies does not effectively avoid bugs for the entire nesting season, because bugs are mobile and do move out of old unused nests and across the substrate to invade new nests. At a 600-nest colony and at a 1000-nest colony, each containing old unused nests, we found that newly built nests had attracted hundreds of swallow bugs by the end of the nesting season. Swallow bugs also hide in crevices of the colony's substrate (Foster and Olkowski 1968, J. Loye, *personal communication*), and may persist at colony sites even if old swallow nests are destroyed by the elements during the fall and winter. The

bugs may then invade new nests that are constructed on that substrate. However, invasion of new nests is not instantaneous, and use of a new nest is probably advantageous for Cliff Swallows in giving them a 1–2 wk “head start” on the bugs. Our results indicate that 1–2 wk may make the difference between fledging young and losing them to bugs. Pressure from swallow bugs probably has had profound effects on the evolution of the Cliff Swallow’s breeding phenology.

Our results suggest that parasitism by the flea *C. celsus* is less costly to Cliff Swallows than parasitism by swallow bugs. Flea infestations probably do not result in measurable fitness reduction, and consequently fleas are unlikely to represent a cost of group living. The fact that the number of fleas per nest does increase with colony size (Fig. 7) but that fleas do not reduce nestling body mass (Fig. 8), suggests that correlations of ectoparasite infestation levels with group size without evaluation of the actual effects of the ectoparasites may be misleading. For example, in a study of Bank Swallows, Hoogland and Sherman (1976) found that infestations of fleas (*C. riparius*) increased with group size and thus concluded that ectoparasitism represents a cost of coloniality for Bank Swallows. But they had no information on the degree to which the fleas affected the swallows, so their conclusion must remain tentative.

Ectoparasitism has important implications for the evolution of sociality in Cliff Swallows. Ectoparasites are responsible for most of the observed nestling mortality, and predation is only a minor factor for these birds (Brown 1985). Without compensating benefits of coloniality, the cost of ectoparasitism would quickly select for solitary nesting in Cliff Swallows. Through complex evolutionary trade-offs between several different benefits and costs of group living, coloniality has evolved and is maintained in these birds (Brown 1985). Given the serious impact of ectoparasitism on Cliff Swallows, ecologists should perhaps pay more attention to the potential effects of ectoparasites on natural populations of other social animals.

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