Parasites and Their Effects On Colonies of Cliff Swallows

Living in Groups Has Some Major Drawbacks

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Photographs by Mary Bomberger Brown

Almost everyone with even a casual interest in animals has undoubtedly noticed that many animals live in groups. Schools of fish, nesting colonies of birds, and roving herds of hoofed mammals are examples of animal groups that have captured the interest of field naturalists dating back to the time of Aristotle. Modern zoologists, more specifically known as behavioral ecologists, who study animal groups have directed most of their efforts at determining what causes these aggregations to form. Research on a variety of animals over the last twenty-five years suggests that there are three major advantages of living in groups. These include the enhanced ability of animal groups to locate and exploit hard-to-find or dangerous food sources, the enhanced ability of animal groups to avoid predators in several kinds of ways, and the enhanced use of scarce resources where many individuals may gather. Study of these advantages of group-living has helped behavioral ecologists to better understand why some animals show pronounced degrees of sociality and why others have largely solitary life styles.

A cliff swallow colony on a cliff face along the shore of Lake McConaughy, Keith Co., Nebraska. The gourd-shaped nests are built entirely out of mud pellets which the birds collect in their bills. When the mud dries, the cantaloupe-sized nests are so solid that they sometimes hold together for five years or longer.

More recently, behavioral ecologists have also become aware that there are not only advantages to group life but also obvious disadvantages. In bird colonies, for instance, it is easy to see how competition for available resources such as food, nesting sites, and mates would increase in the larger colonies where more individuals are present. Such competition can have serious consequences for the members of the group that do not compete effectively, and the competition itself may be costly in terms of time and energy expended even to the winners within the group. Another disadvantage of colonial life is an increased probability of encountering ectoparasites or disease-causing bacteria or viruses (also known as pathogens) introduced by other group members. One only has to consider the proverbial child who immediately comes down with a cold or chicken pox as soon as he or she goes back to school, to appreciate the potentially very heavy cost of living in groups where disease and parasites may thrive! Behavioral ecologists are now beginning to realize that both the advantages and disadvantages of group-living must be explored if we are to understand properly the evolution of animal sociality.

Since 1982, my own research has focused on the advantages and disadvantages of group-living in a highly colonial bird, the cliff swallow (*Hirundo pyrrhonota*). This species, which is the same one that mythically returns to San Juan Capistrano on the same day each year, is one of the most highly colonial land birds in North America. It breeds in colonies of up to 3000 nests each. Here I wish to discuss the ectoparasites—parasites living on the exterior of the host—which are associated with cliff swallows. My studies over the last four years clearly show that the effects of ectoparasites represent the most important disadvantage of group-living to these birds. More importantly, my research has suggested that the effects of ectoparasites may in general be greatly underrated and that parasites may have tremendous effects in many ways on natural populations of wild animals.

The Natural History of Cliff Swallows

Cliff swallows nest in colonies throughout most of western North America, and they are one of the most abundant swallows west of the Great Plains. The species formerly occurred in parts of New England and in other areas of the eastern United States, but usurpation of their nests by introduced European house sparrows (*Passer domesticus*) has

An adult cliff swallow (left) and its recently fledged chick (right). Adults have conspicuous white foreheads, orange rumps, and square tails. The adult here is preening the feathers of its back, possibly in response to large numbers of ectoparasites that attack these birds.

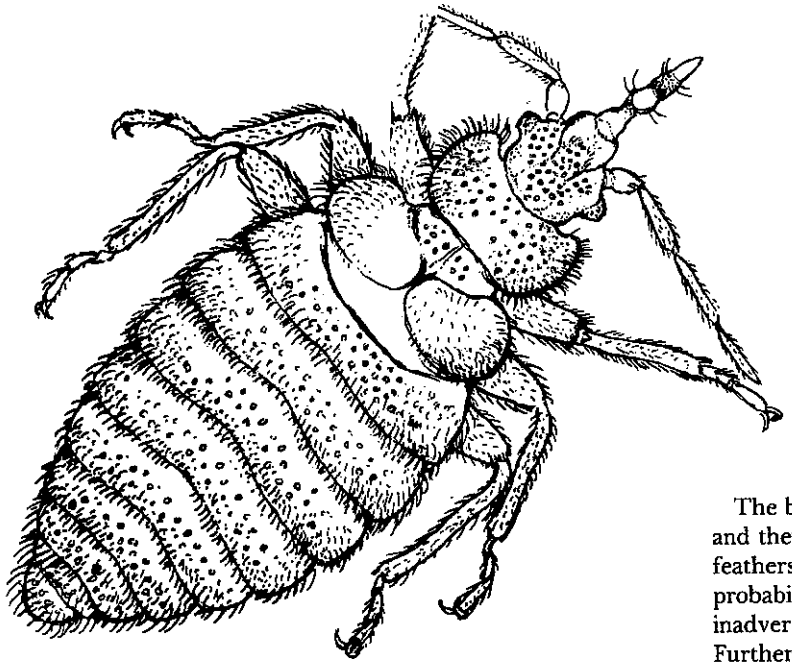
drastically reduced cliff swallow populations in much of the East. Cliff swallows arrive in the southern and coastal parts of their breeding range in March and arrive in most other areas by early May. Most cliff swallows leave North America in August and September for their wintering range, which extends from southern Brazil to Argentina and Chile. These 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 rough vertical substrate (or base) for attaching nests. These birds are aerial insectivores and feed exclusively on insects caught in flight. Prolonged late spring cold snaps occasionally kill large numbers of cliff swallows when such weather reduces the available aerial insects upon which the birds depend.

Cliff swallows occur in a wide variety of habitats. Open fields for feeding and a body of water serving as a mud source for nest-building are usually located reasonably close to each colony. This species commonly nests from semiarid grasslands up to pine-oak forests at about 9000 feet but rarely at higher altitudes. Cliff swallows are highly social in all of their activities, feeding, preening, migrating, gathering mud for their nests, and loafing in large and highly synchronized flocks. Nesting within each colony is also highly synchronized, with most individuals beginning their nests within a period of a week or less, even in colonies of several hundred birds.

Cliff swallows are sparrow-sized birds with an obvious orange rump and a white forehead patch. Their tails are square, unlike the forked tails of the closely related barn swallows (*Hirundo rustica*) with which cliff swallows are often confused. Barn swallows, which are far more common in the eastern United States than cliff swallows, also build nests out of mud and nest under the eaves of buildings. Barn swallows, however, are much less social than cliff swallows, and barn swallow colonies seldom contain more than ten nests.

Study Area

My research is conducted in the beautiful sandhills of southwestern Nebraska at the University of Nebraska's Cedar Point Biological Station near Ogallala in Keith County. This region, one of cattle ranching and agriculture, is admirably described in John Janovy, Jr.'s critically acclaimed book, *Keith County Journal.* Cliff swallows are abundant in southwestern Nebraska and have probably always occurred there, nesting on bluffs and outcrops along the North Platte River. They have likely increased in recent years with the construction of artificial structures (such as bridges and culverts) upon which they can nest. My field assistants and I study colonies that are 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, the largest lake in Nebraska. Through 1985, we had studied 167 cliff swallow colonies, totalling more than 53,000 nests. The average colony size in this study area is about 300 nests, and colonies range in size from 1 to 3000 nests.



Parasitism by Swallow Bugs

Throughout their range, cliff swallows are associated with many blood-sucking ectoparasites. These parasites include ticks, fleas, true bugs, and flies. The parasitic fauna that afflicts cliff swallows varies considerably in different parts of the bird's range, with the more southerly populations in general being more heavily affected (probably because of the mild winter weather in the South that allows ectoparasites to better survive the winter months). Parasitologists are beginning to unravel these parasites' complex and highly interesting life cycles which have enabled these creatures to become (in most cases) specialized cliff swallow parasites. The birds' mud nests, which in well-protected locations may hold together for many years, create favorable environments for survival and reproduction of the ectoparasites. Cliff swallows reuse old nests from year to year, and as a result the birds' continued association with the ectoparasites is facilitated.

The most numerous cliff swallow ectoparasite in southwestern Nebraska is the swallow bug (*Oeciacus vicarius*), a bloodsucking hemipteran closely related to and physically resembling the human bedbug. These long-lived ectoparasites spend most of their lives within cliff swallow nests and within cracks and crevices in the surrounding cliff face or bridge wall to which the nests are attached. These bugs can perhaps survive up to three or more years without feeding, which means that they are well adapted to irregular colony site usage by their cliff swallow hosts. Cliff swallows often skip one or more years between use of a given colony site, and during this period of time the bugs apparently fast. As soon as the birds reoccupy a colony early in the spring, the bugs immediately become active, feed, and reproduce. Their reproduction is closely synchronized with the eight-to-ten-week period during which cliff swallows occupy the colonies.

The bugs, however, do disperse from colony to colony, and they do this by clinging to the bases of the cliff swallows' feathers. Thus, as more birds colonize any given site, the probability that some swallows carrying bugs will arrive and inadvertently introduce these bugs to that site, is increased. Furthermore, as a colony's size increases, so does the number of physical contacts among different individuals and different nests. My assistants and I, therefore, predicted that one potential disadvantage of coloniality in cliff swallows is increased transmission of ectoparasites. We set out to examine whether infestations of swallow bugs increased in large cliff swallow colonies and whether these infestations affected the birds in any way.

We first investigated whether the number of bugs present per nest varied with colony size. We did this in two ways. One way was to remove nestling cliff swallows when they were 10 days old and count the number of bugs that were attached to the nestlings. Nestlings were examined and then returned to their nests. This was done in colonies of different sizes, and we did this for over 2000 nestlings. And since the nocturnal bugs often hide in the nest materials during daylight hours and thereby avoid any diurnal contact with the nestlings, we also collected nearly 300 entire cliff swallow nests shortly after the nestlings fledged. We sifted through these nests by hand and laboriously counted all of the bugs present in each nest.

As we predicted, the number of bugs per nest increased significantly with colony size. Some nests in the largest colony we studied contained over 2500 bugs each, and some nestlings in these colonies had over 80 bugs attached to them! At times, parasite infestations in the larger colonies were truly phenomenal, with thousands of bugs crawling on the outside of each nest and on the surrounding substrate. We also discovered that rates of parasitism increased later in the season, and swallow nestlings hatched late in the summer often literally were completely drained of their life's blood by the swallow bugs.

Given the increased parasite loads in the larger cliff swallow colonies, we then investigated to what degree the parasites actually harmed the birds. For birds that nested late in large colonies, it was clear that mortality caused by bugs was nearly 100%. But we wished to learn if there were other less drastic, but still consistently negative, effects for the remaining majority of cliff swallows.

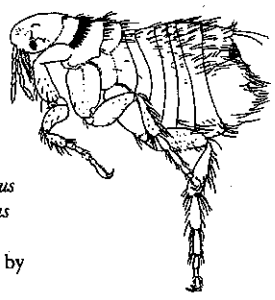
We performed a field experiment to investigate the effects of swallow bugs. We selected seven colonies of different sizes, divided each one in half, and fumigated half of the nests there with a short-lived fumigant, Dibrom®. This fumigant had no detectable effects on cliff swallows but was highly effective against swallow bugs, killing them immediately. We applied the fumigant as a fine mist to the outside of swallow nests at regular intervals throughout the season. After the nestling cliff swallows hatched, we weighed each nestling at ten days of age and determined how many nestlings had survived. This was done for the fumigated and nonfumigated nests in each colony.

Our results showed clearly that there were consistent effects on nestling cliff swallows attributable to swallow bugs. In the small colonies, there were no differences in nestling weight and survivorship between fumigated and nonfumigated nests. This was exactly as we had predicted, because in small colonies effects of bugs are not expected to be great since there are so few bugs present. But in the large colonies that contained many bugs, the difference between fumigated and nonfumigated nests was striking: body weights of nestlings in the nonfumigated nests that were exposed to natural levels of bugs were about 20% less than those of nestlings in the fumigated nests, and survival of nestlings in nonfumigated nests was only half that of nestlings in fumigated nests. These effects tended to increase consistently across all colony sizes. Furthermore, we found that in subsequent years, more birds raised in fumigated nests returned to our study area than birds raised in nonfumigated nests, suggesting that annual survivorship may be greater for parasite-free birds.

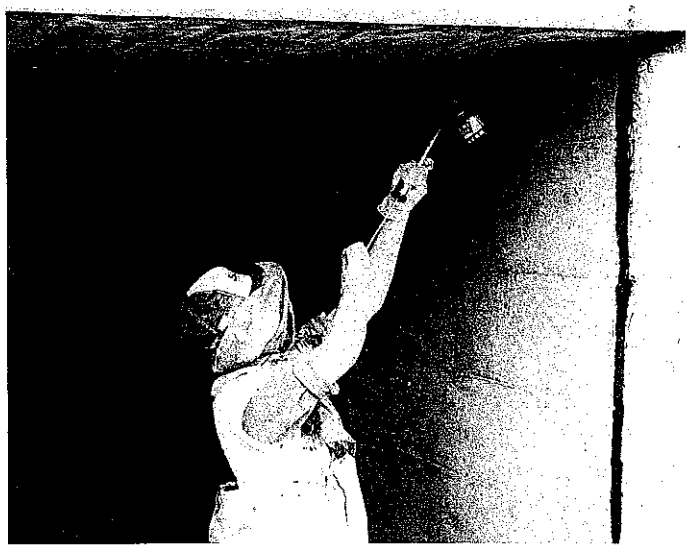
This research has clearly shown that parasitism by swallow bugs represents a major disadvantage of living in groups for cliff swallows. The effects of swallow bugs are compounded by the fact that bugs are not the only parasites that cliff swallows in Nebraska must contend with. There are also fleas.

Parasitism by Fleas

The second most numerous cliff swallow ectoparasite in our study area is a bird flea (*Ceratophyllus celsus*). Like the swallow bug, fleas reproduce within swallow nests. The flea larvae feed on detritus within the nest over the winter, and these larvae-turned-adults await the birds upon their return in the spring. Fleas cluster at the entrances of swallow nests where they leap onto passing cliff swallows. Fleas are more mobile than swallow bugs, and must find a host each spring to survive. If a colony is ignored by the birds for a season and no swallows visit it, virtually all of the fleas stranded there will die. Adult fleas are unable to fast for multiyear periods, unlike swallow bugs.



Swallow bug (opposite page, *Oeciacus vicarius*) and flea (right, *Ceratophyllus petrochelidoni*)—two of the parasites that attack cliff swallows. Drawings by David Kiphuth.



One of the author's field assistants fumigating cliff swallow nests in a highway culvert as part of an experiment to determine the effects of swallow bugs on nestling cliff swallows. The researcher's head is wrapped in mosquito netting to avoid hordes of biting black flies that also lived in this culvert.

We predicted that fleas might increase in larger cliff swallow colonies because more would be introduced there and their spread enhanced, just as for swallow bugs. Early each spring, fleas cluster at the tube-shaped entrances of cliff swallow nests, waiting for a passing host. We sampled their populations in different sized colonies by tricking them into "thinking" that a host was present. We did this by placing a black index card, coated with honey, over the entrance of each cliff swallow nest. The card mimicked a bird's blocking of the entryway and stimulated the fleas (whose poor vision consists mainly of just distinguishing light and dark) to jump at the card. The fleas were then trapped by the honey and counted by us. This gave us a sample of the fleas per nest in different-sized colonies.

We card-sampled fleas at over 300 nests early in the spring just before the cliff swallows returned to the study area. Nests in small colonies had no fleas, while ones in large colonies had up to thirty-nine fleas each. Infestations of this ectoparasite also increased significantly with cliff swallow colony size.

However, we found that fleas actually had little effect on the nestling swallows. When we examined the number of fleas per nest and the weight of the corresponding nestling cliff swallows, we found surprisingly that nests with more fleas tended to contain slightly *larger* nestlings. This indicated that the fleas, although increasing in large colonies, were probably not affecting the nestling cliff swallows in any harmful ways. We are unsure if the fleas might have greater, and as yet unknown, effects on adult swallows, and that is a possibility. But in general, at this time, it does not appear that fleas are as costly to cliff swallows as the swallow bugs.

The Avoidance of Ectoparasitism

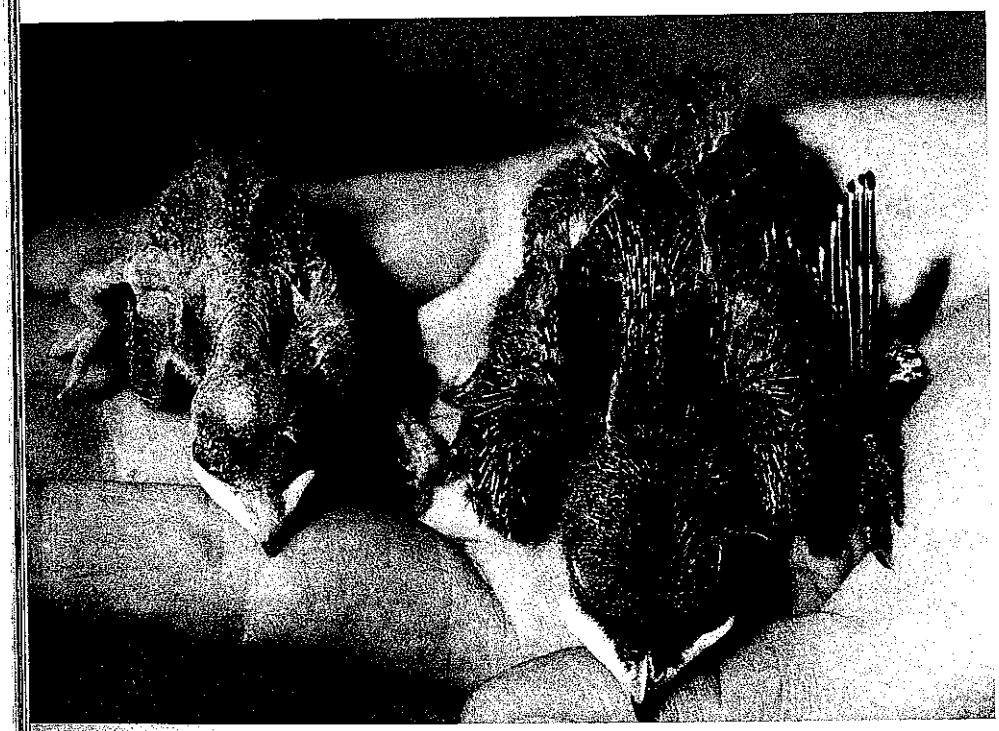
Many parasitologists argue that parasites seldom affect their hosts in drastic ways. If parasites were to kill off their hosts, that obviously would not be adaptive for the parasites themselves. The cliff swallow story suggests caution in applying that logic. Swallow bugs definitely kill off their hosts in the larger cliff swallow colonies. This may be an example in which competition among the parasites forces each one to grab as much of the host-resource as it possibly can as quickly as it can, even though this does lead to loss of the host in some cases. Nevertheless, host-parasite systems such as this with such drastically, and such consistently, deleterious effects on the hosts are apparently quite rare. Deleterious effects of ectopar- asites on cliff swallows are not confined to Nebraska; similar effects have been reported in cliff swallows in Texas. And in Oklahoma bug infestations per nest may be at least double what we observed in Nebraska!

Given the substantial disadvantages of swallow bug parasitism, one might expect cliff swallows to exhibit behavior to minimize the parasites' effects. The most effective behavior for avoiding bugs may be to use colony sites in alternate years. Although some bugs can fast and might survive in unused nests for up to three years, many bugs do die the winter following a season of colony use. If a colony stood vacant for an entire year, by the end of the second winter, populations of swallow bugs might be substantially reduced. Observed patterns of cliff swallow colony site usage in a number of areas are indeed erratic, with birds often skipping one or more years between use of a given site. This is consistent with the interpretation that this behavior is a means of avoiding bugs.

Furthermore, my assistants and I observed patterns in the birds' use of nest sites within two Nebraska colonies that strongly suggest that cliff swallows are able to accurately assess ectoparasite loads from the previous year before selecting which nest sites to use early in the spring. In early spring of the year after we performed our fumigation experiment, substantial numbers of old nests remained, largely intact, in the two largest colonies in which we had fumigated nests the previous year. As soon as cliff swallows arrived in the study area, 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, even though both kinds of nests were in some cases separated by less than two feet! That year we maintained the previous fumigation scheme at one of these colonies, only spraying nests that had been previously fumigated. No cliff swallows ever used any of the nonfumigated nests that year at that colony. However, at the other colony we began fumigating the *entire* colony several weeks after the birds had established initial occupancy of the nests. Although birds that year had previously showed virtually no interest in the nonfumigated nests at that colony, hundreds of birds began nesting in all sections of the colony scarcely a week after the total fumigation began.

These experimental results from two colonies indicate that cliff swallows do at times assess relative degree of ectoparasite infestation among nests in colonies early in the year and that parasite-free nests are quickly occupied. The birds probably evaluate the degree of parasitism by hovering in front of the nests and seeing the fleas and swallow bugs clustered in plain sight at the entrances of the nests. Cliff swallows also probably continually assess the degree of parasitism within their colonies as the nesting season progresses. When parasite loads toward the end of the year become prohibitive and successful reproduction is unlikely, they abandon their nests and desert the colony. We have observed several instances in which up to 200 nests containing eggs and nestlings in some colonies were abandoned late in the year when bug infestations became severe.

Why do cliff swallows put up with the bugs at all? Why not disperse and avoid bugs by nesting solitarily in the same fashion as barn swallows? The answers to these questions are complex, but may be summarized by noting that there are advantages to nesting in colonies too, and these advantages on average at least balance the disadvantages. The most



Typical nestling cliff swallow from a nonfumigated nest (left) and from a fumigated nest (right) at a 345-nest colony. Both were the same age (10 days). The cost of being parasitized is obvious.

important advantage of group-living for cliff swallows is enhanced ability to find food through group feeding. Individuals within a colony use other individuals to learn the current location of food sources, and the resulting enhanced foraging efficiency balances, evolutionarily speaking, the effects of ectoparasites. The system through which cliff swallows forage socially is a complex one, and will have to await future issues of *Discovery*.

Conclusion

In the past, many field naturalists have tended to emphasize predation as one of the most important causes of the mortality observed in natural populations of animals. In contrast, this study of cliff swallows suggests that ectoparasitism by swallow bugs accounts for much of the observed mortality in this species, and in fact, predation is only a minor factor for these birds. These results, I think, imply that the potential effects of parasites and pathogens should be examined fully for other species of animals, and in particular, group-living animals. Parasites may well prove in general to be a big disadvantage of group-living and may exert a measurable influence on the evolution of animal sociality. More importantly, parasites may also represent a major ecological force that shapes the structure and distribution of wild animal populations.

Acknowledgments

Without the assistance of Mary Bomberger Brown, this research could not have been done in nearly so complete a fashion. Mary has been involved in all aspects of this project since the very beginning. For dedicated field assistance, I thank Cathy Boersma, Carol Brashears, Karen Brown, Rachel Budelsky, Laurie Doss, Laura Jackson, Deborah Johnson, Kathi Miller, and Todd Scarlett. John Janovy, Jr. and the University of Nebraska's School of Biological Sciences allowed my assistants and me to use the facilities of the Cedar Point Biological Station. Cluff Hopla developed the method for sampling fleas. My parents, Raymond and Kathryn Brown, helped in many important ways. My research has been supported by the National Science Foundation, Princeton and Yale universities, the American Museum of Natural History, the National Academy of Sciences, Sigma Xi, and Alpha Chi.

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