Photo by Charles R. Brown.

Cliff swallows perched at their gourd-shaped mud nests in Keith County, Neb. With a lifespan of up to 12 years, this species is one of the most social land birds found in North America.

How Cliff Swallows Choose Where to Live

By Charles R. Brown

One of the most spectacular natural phenomena in the springtime in North America is the annual return of millions of migratory birds to their nesting grounds in the forests, marshes, prairies, lakes, deserts, and cities of temperate latitudes. More than 80 percent of all North American birds migrate, according to some estimates, with some species commuting thousands of miles to milder climates. That many of these migrant birds return, rather remarkably, to the original nesting territory, sometimes even to the same nest tree or birdhouse, that they had occupied the previous year almost strains credulity.

No less striking is the habit of many birds to appear at their breeding grounds at about the same time each spring. One of the most famous examples is the punctual arrival of the fabled cliff swallows (*Petrochelidon pyrrhonota*) at Mission San Juan Capistrano in San Juan Capistrano, Calif. Legend has it that these sparrow-sized birds, in a migration from their wintering range 6,000 miles away in Argentina, return annually to the hallowed grounds on March 19, St. Joseph's Day (a Roman Catholic commemoration of the stepfather of Jesus and husband of the Virgin Mary). There they build gourd-shaped mud nests under the eaves of the buildings. The mission, founded in 1776 (for more about it, go online to http://www.missionsjc.com), celebrates this event widely, drawing thousands of tourists and national media coverage, and the Capistrano swallows have inspired songs, poetry, and books.

Unfortunately, in recent years the swallows have not returned to Mission San Juan Capistrano, breaking their centuries-old habit and occupying other places nearby. As a result, perplexed mission-goers and swallow enthusiasts ask what would cause the birds to abandon one nesting site and choose another; what makes a site attractive to a cliff swallow; and, most importantly, will these birds ever resume breeding at the mission?

I can't answer the last question, but for almost 30 years my quest has been to understand why cliff swallows choose one nesting site over another. In the process of studying cliff swallows in western Nebraska — this species occurs commonly throughout western North America and more sporadically farther east — I have gained insight into how evolution shapes animals' decision-making. What appears sometimes to be random, almost capricious decisions by animals to settle in one spot over another are often the results of relatively simple behavioral rules of thumb that individuals follow predictably: those who did so in the past were more successful at producing offspring and were favored by natural selection.

Cliff swallows, in other words, have proven to be marvelous animals for exploring the complexities involved in choosing where to live, a decision that millions of migratory birds are faced with annually upon their springtime return to the breeding grounds.

Why do birds flock together?

My interest in cliff swallows was not motivated by a desire to restore them to San Juan Capistrano (although in 2001 I did consult with the mission on ways it might re-attract the birds). Rather, my curiosity stemmed from a fundamental question that has intrigued evolutionary biologists and ornithologists for centuries: Why do birds like cliff swallows form large nesting colonies? Indeed, some cliff swallow colonies in the western Great Plains exceed 6,000 nests on a single bridge, the nests packed densely underneath beams in dry, protected spots safe from predators and inclement weather.

In 1982, I set out to answer that question and determine whether cliff swallows formed colonies to escape attack from predatory birds or snakes, or, alternatively, to find food through "information transfer," a process whereby individuals learn from watching other group members where hard-to-find food can be found.

Behavioral ecologists such as Ron Pulliam, John Hoogland, and Paul Sherman thought colonial nesting evolved because group living enabled animals to avoid predators more effectively through greater vigilance (seeing the predator sooner gives you longer time to escape), better deterrence (a mob of screaming, diving birds can dissuade a predator from attacking), or favorable odds (being statistically unlikely to be the predator's victim even if it attacks the colony).

Other scientists including Amotz Zahavi, John Krebs, and Stephen Emlen proposed that living together also aids in the search for food, particularly when animals feed on patchy or ephemeral resources. Simply put, if it takes a long time for an animal group to find a food source (such as a school of fish in the sea or a swarm of insects in the air), individuals can avoid the costs in time and energy of searching for food themselves by instead watching where others in that group feed and then following suit. A large group typically contains at least one member that happens to know the whereabouts of a food patch at any particular time; so unsuccessful members can simply observe others and benefit as a result.

Evidence gleaned from my extended studies — of more than 200,000 banded cliff swallows in almost 200 colonies in western Nebraska, where the species is more abundant than virtually anywhere else on the continent, according to the North American Breeding Bird Survey — verifies

Photo courtesy of Mission San Juan Capistrano.

The bell wall at Mission San Juan Capistrano, a famous site to which cliff swallows annually return — historically but not recently.

Cliff swallows in western Nebraska nest underneath the sides of highway bridges; in concrete, box-shaped culverts underneath roads and railroad tracks; under eaves of buildings; and beneath overhanging ledges on natural cliff faces …

the latter hypothesis: the primary reason cliff swallows live in groups is to increase their food-finding ability.

Feeding on swarms of small insects whose occurrence is unpredictable even from hour to hour, these birds learn where food can be found from other colony members. (Birds vary in whether they happen to be the one who knows where the food is at a given time or the one who follows after others; thus, each bird in the colony seems to benefit equally over the long term.) The consequence is that cliff swallows living in groups have higher foraging success than those living alone or in small aggregations — explaining generally why they form colonies in the first place.

Bugs impact birds' nesting

Bigger mysteries about cliff swallow biology are why colonies vary so much in size (nesting groups range from a few birds to thousands of them) and what determines whether a colony site is used by birds in a given summer. Some birds, despite foraging-related advantages of living in big groups, choose to live solitarily. Others settle in colonies that may be tiny or enormous. And birds that occupy one colony site may suddenly abandon it and move elsewhere, as exemplified by the situation at San Juan Capistrano. We are just now beginning to unravel the complexities of what determines where cliff swallows settle and with how many other birds.

Cliff swallows in western Nebraska nest underneath the sides of highway bridges; in concrete, box-shaped culverts underneath roads and railroad tracks; under eaves of buildings; and beneath overhanging ledges on natural cliff faces (their ancestral home that they have largely forsaken). One factor that was obvious early in my research is that the presence of ectoparasites, parasites that live on the exterior of another organism, influences the birds' settlement patterns.

Being a social species, cliff swallows are exposed to a wide variety of parasitic and pathogenic organisms, including ectoparasitic fleas and bugs and some arthropod-transmitted viruses. Increased contact with parasites is thought to be an unavoidable cost of group living for all animals. The principal parasite of cliff swallows in western Nebraska is the swallow bug (*Oeciacus vicarius*), a blood-sucking insect that is the size of a large tick and that has many taxonomic and ecological similarities to the human bedbug.

Swallow bugs live year-round in the swallows' mud nests and feed on the sleeping adult birds at night and on the helpless nestlings throughout the day. Up to 2,600 bugs can be found in a single nest, and the total swallow bug population at some of the largest colony sites can exceed half a million. Fellow behavioral ecologist Mary Bomberger Brown and I established that the number of bugs per nest increases with colony size, meaning that cliff swallows have to contend with more bugs, on average, if living in large groups. Furthermore, observations and experiments proved that bugs exert a serious toll on these birds: if infestations are high, nestlings can die from loss of blood, and even those babies that survive initially are less likely to live to the next year.

The bugs do not travel on the cliff swallows when the latter migrate; instead, the bugs overwinter in the birds' nests. Therefore, the bugs are waiting for the birds when the cliff swallows return each spring. Cliff swallows assess the number of bugs in nests, flying to the front of a nest, hovering there but not entering, and apparently looking for bugs that lurk in

the nest's interior recesses. If a site was heavily infested the previous year, many bugs are likely to remain the next spring, and so the cliff swallows abandon it.

Fumigation experiments, in which collaborators and I killed the bugs in half of the nests in a colony, confirmed the aforementioned premise. All the fumigated nests were reoccupied the following spring, but virtually none of the infested nests were used within the same colony. At colony sites where all the nests were fumigated perennially, the number of birds nesting there increased by several hundred nests each year until the colony reached an apparent capacity within a few years.

Thus, one determination about where cliff swallows settle each spring is the parasite legacy they would inherit from the previous year. Whether they decide to return to any given nesting location will depend at least in part on how many bugs are able to survive the winter.

Nothing in the field is simple, though, and bug survival seems to vary widely among sites. Factors include the microclimate of the nesting substrate, the base on which an organism lives (bugs don't survive as well on cold metal as on concrete); the severity of the winter; and the reproductive rates of bugs the previous summer. Although bugs influence the swallows' choice of colony, predicting how many bugs will be at a particular colony site and, thus, whether cliff swallows will return there each spring, is not something I can do with certainty even after 30 years of study!

Photo by Kristen Lear, 2008, courtesy of the author.

Charles R. Brown extracted cliff swallows from a mist net erected in front of a road culvert near Keystone, Neb., where the birds were nesting, in order to band them.

Photo by Mary Bomberger Brown.

Brown collected swallow bugs from cliff swallow nests at a colony on a bridge over the North Platte River at Broadwater, Neb., in July 2005. Bugs can represent a serious cost of clustered nesting when their numbers increase in large colonies, as was the case with this one.

Nature, as much as nurture, guides birds

Cliff swallows are similar to many other bird species in that they all have one simple rule: if unsuccessful at one place, avoid it in the future. If birds lose their nest, eggs, or young to predators, parasites, or storms, they immediately abandon the site for good. Natural selection favors those cliff swallows who never forget, whether in western Nebraska or San Juan Capistrano, Calif.

On the other hand, familiarity with a particular area does have advantages. Collaborators and I found that individual birds that had settled at the same Nebraskan breeding colony site in previous years were more likely to survive the summer nesting season than were those that had lived elsewhere in the past and were therefore naïve about their new surroundings. Knowing where food is apt to be found during times of scarcity (such as in late spring cold snaps) or what the hunting habits of local predators are apparently confers some real advantages to cliff swallows.

Perhaps the most surprising discovery about how cliff swallows choose where to live was the realization that colony size is, in part, based on genetics. It is well-known that some animals produce increased levels of stress hormones in social situations, and some 15 years ago I guessed that cliff swallows might "perform" better (i.e., be successful in raising young) when in groups of different sizes. Few colleagues, however, thought that an individual's choice of what size group it would live in could be determined by genes.

To determine if there were innate preferences for groups of particular sizes, colleagues and I embarked in 1997 on an experiment in which some nestlings born in a Nebraskan colony of one size were raised in a colony of a very different size. We had monitored when nestling cliff swallows hatched, and as soon as they were old enough (3-4 days), we banded them for permanent identification. We then switched some babies born in large colonies to nests in small colonies to be raised by foster parents; we did the reverse as well with additional hatchlings.

If the babies' subsequent choice of where to live was based largely on genetic tendencies, the youngsters should later choose colonies that matched in size where they were born (where their parents chose

Photo by Charles R. Brown.

Cliff swallow nests are shown on the side of a cliff along the shore of Lake McConaughy, Neb., in May 2005. The birds historically used these sorts of nesting sites but in recent decades have switched to nesting mostly on highway bridges, in culverts, and under eaves of buildings.

Photo by Valerie A. O'Brien, courtesy of the author.

The author fumigated cliff swallow nests to remove swallow bugs at a colony in a culvert underneath a road near Keystone, Neb., in July 2008. The birds have higher nesting success in colonies where bugs are removed.

to live), not where they were reared. On the other hand, if early experience as a fledgling in a particular social environment dictated later choices, the exchanged birds should choose colonies that matched the size of the sites where they were reared.

The next summer we caught breeding birds, looking to see where our experimental birds returned and what size colonies they chose as first-time breeders. Yearling cliff swallows chose breeding colonies that matched in size with where they were born and rarely occupied sites similar to where they were reared. Thus, cliff swallows seem genetically programmed to use colonies of a particular size.

This hard-wired instinct may account in part for where some birds settle each spring upon their return.

Tenets apply; enigmas remain

We have only scratched the surface of understanding what causes animals such as cliff swallows to choose to live at a particular place, at a particular time, and with a particular number of individuals. Yet certain rules do apply for birds: Avoid parasites, live in familiar areas unless you fail to reproduce there, and settle in colonies of size similar to your parents.

With these rules in mind, it may be possible to understand better why the songbirds that nested in your yard last year either returned or moved elsewhere this spring. Few choices an animal makes are more important than where to breed, and at least for cliff swallows, few things they do are as complex. We may never know why the swallows seemed to have given up on their longtime home at the San Juan Capistrano mission, but we can say with certainty that they are following rules of behavior that natural selection devised. ■

Charles R. Brown, Professor of Biological Sciences at University of Tulsa, has studied swallows since age 11. Over the last 28 years at field sites in western Nebraska, he and a research team have marked and studied more than 200,000 cliff swallows. Brown published his first scientific paper at age 15 and articles he wrote or co-wrote have appeared in *Nature*, *Science*, *Evolution*, and *Ecology*, among other publications. Brown also serves as associate editor of *Behavioral Ecology and Sociobiology*. From 1986 to '93, he was curator of ornithology at the Peabody Museum of Natural History at Yale University, where he once taught. In 2009, Brown and collaborator Mary Bomberger Brown of the University of Nebraska-Lincoln received the Elliot Coues Award from the American Ornithologists' Union in recognition of their research on cliff swallows. He earned biology degrees from Austin College (B.A.) and Princeton University (Ph.D.). Email him at charles-brown@utulsa.edu.

Additional Reading on Swallows

● Brown, C. R., and Brown, M. B., *Coloniality in the Cliff Swallow: The Effect of Group Size on Social Behavior*, University of Chicago Press, 1996. 566 pp.

This scholarly monograph summarizes the first 12 years of my cliff swallow project in Nebraska and presents one of the most detailed studies of coloniality in any animal.

● Brown, C. R., *Swallow Summer*, University of Nebraska Press, 1998. 371 pp.

This book, targeted for nonscientists, describes the joys and frustrations of a summer in the field studying cliff swallows.

● Brown, C. R., and Brown, M. B., "Heritable Basis for Choice of Group Size in a Colonial Bird," *Proceedings of the National Academy of Sciences USA* (2000) 97: 14825-14830.

This paper describes studies on heritability of colony size choice in cliff swallows.

● Brown, C. R.; Brown, M. B.; and Brazeal, K. R., "Familiarity with Breeding Habitat Improves Daily Survival in Colonial Cliff Swallows," *Animal Behaviour* (2008) 76: 1201-1210.

This paper explains studies on the survival advantages of cliff swallows that occupy familiar colony sites.

● Emlen, J. T., Jr., "Social Behavior in Nesting Cliff Swallows," *Condor* (1952) 54: 177-199.

This was the first detailedstudy to describe the highly social nature of the cliff swallow.

● Hoogland, J. L., and Sherman, P. W., "Advantages and Disadvantages of Bank Swallow (*Riparia riparia*) Coloniality," *Ecological Monographs* (1976) 46: 33-58; and Snapp, B. D., "Colonial Breeding in the Barn Swallow (*Hirundo rustica*) and Its Adaptive Significance," *Condor* (1976) 78: 471-480.

These two pioneering studies on swallow sociality were done on species related to cliff swallows.

● Safran, R. J., "Adaptive Site Selection Rules and Variation in Group Size of Barn Swallows: Individual Decisions Predict Population Patterns," *American Naturalist* (2004) 164: 121-131.

This recent study examines how the barn swallow, closely related to the cliff swallow, chooses colony and nest sites.

— Charles R. Brown