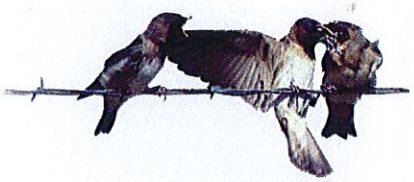
Two ornithologists who come to Nebraska each year to study cliff swallows witness natural selection in action

Seventeen Summers of Swallows

Words and Photographs by Charles R. Brown

As I stepped out of the brush along the river bank and onto a wide open sandbar in the middle of the South Platte River bed, I saw dozens of cliff swallow corpses littering the sand. Farther away, many more floated in a stagnant backwater pool. Above me towered the highway bridge connecting Interstate 80 to Ogallala, the former frontier town touted as "where

Birds on a wire.
Cliff swallows can't seem to find a solitary moment. It's all work, work, work. At right, a parent feeds a fledgling a tasty meal of stomach contents. Below left, the high-density housing in which cliff swallows congregate makes a fine defense against predators, and a nurturing breeding ground for parasites.



THE WEST BEGINS." HUNDREDS OF VACANT CLIFF SWALLOW NESTS LINED THE UNDERSIDES OF THIS BRIDGE. SIX DAYS AGO, MORE THAN A THOUSAND SWALLOWS HAD LIVED THERE. TODAY I SAW TWO BIRDS FLY OVERHEAD, AND MY ASSISTANT KARA AND I WERE ABOUT TO FILL TWO PLASTIC TRASH BAGS WITH MORE THAN 300 DEAD CLIFF SWALLOWS FROM THIS SITE ALONE. MORE DEAD ONES—INACCESSIBLE TO US—HUNG OUT OF THEIR NESTS IN GROTESQUE POSES.

This horrific scene was the result of a late spring cold snap. Cliff swallows eat flying insects, and when the weather is cold and rainy, insects aren't active. The birds simply can't find enough to eat, and they starve to death. If cold weather lasts only two or three days, as it normally does, the birds have enough body fat to be able to fast, and they can survive. But cold weather of six days, especially at the end of May, was highly unusual. We were witnessing an event which had occurred only twice in the last 125 years. Yet as Kara and I grimly filled up our trash bags, my only concern was how this massive mortality would affect the research on cliff swallows that my wife, Mary Bomberger Brown ('79, G'82), and I had been conducting in the Ogallala area since 1982. There was the real chance that there would be no more birds for us to study.

Our headquarters for the past 17 years has been the Cedar Point Biological Station, run by NU's School of Biological Sciences. Perched on a bluff nine miles north of Ogallala and overlooking the North Platte River Valley and the Sand Hills, it offers summer field courses to college undergraduates and, as I found, unparalleled research opportunities for visiting investigators like me and Mary, whom I met at Cedar Point when she joined the project in its first year.

ENORMOUS COLONIES

I started coming to Nebraska when I was a first-year graduate student, drawn by the cliff swallows, one of the most fascinating animals in the world and whose peak abundance is in the western Platte River Valley. Cliff swallows are recognized by their square tail (unlike the forked tail of most other swallow species), orange rump and prominent white forehead patch. They are surprisingly colorful birds with a dark chestnut throat, a deep—almost metallic—blue head and back, and a cream-colored breast and belly. The cliff swallow builds an enclosed mud nest usually in an enormous colony, traits that distinguish it from the similar barn swallow with which it is often confused. Barn swallows are more likely to nest in farmyards or on human dwellings, and are more widely distributed and thus familiar to more people than are cliff swallows.

Cliff swallows are unusual in being highly social, their gourd-shaped mud

nests clustered together tightly like beehives or wasp nests. They do everything as a group, including feeding, and they migrate between their Nebraska summer home and their winter quarters in Argentina in large flocks. When I started my study, I could never have imagined that this obscure little bird the size of a sparrow would prove so interesting and truly become my life's obsession.

Originally a bird of western North America that nested underneath rocky horizontal overhangs on the sides of steep cliffs and canyons, the cliff swallow has adapted well to modern day environments and human structures. Many of the birds now live under the eaves of bridges or buildings and inside concrete highway culverts, often in rather urban settings. I was surprised to find cliff swallow colonies on virtually every bridge over the North and South Platte rivers, in many of the highway culverts along Interstate 80 and U.S. Highway 26, and on the many bridges and irrigation structures associated with the Nebraska Public Power District's canals. We even found some birds using natural cliff sites along the south shore of Lake McConaughy and along the North Platte River west of Lewellen.

COMPLEX SOCIAL LIFE

As Mary and I began surveying most of Keith, Garden and Lincoln counties over the ensuing years, we discovered more than 150 different sites where the birds nest and a population of at least 75,000 cliff swallows in that area alone. The total number of cliff swallows using the whole Platte Valley during the summer rivals or exceeds that of the more famous sandhill cranes that stop over in the spring.

We also discovered that the simple question we first asked—why do cliff swallows live in colonies—was not so simple after all. The cliff swallow's social life is complex, with advantages and disadvantages. For example, swallow colonies present virtually unlimited opportunities for brood parasitism, that is, the laying of eggs in neighboring birds' nests. We observed birds sneaking into the nests of their close neighbors and laying eggs there, then innocently returning home to care for other eggs themselves. Even more unusual, these swallows physically move eggs in their bills from their own nests into neighbors' bungalows, another way to foist off an egg into the care of others. Egg transfer is virtually unknown among other bird species.

We found other important consequences of the cliff swallow's colonial lifestyle. One is the cost that another kind of parasite poses for these birds. The nests are often infested with parasitic insects that live in cracks and crevices of the mud nest and come out mostly at night to suck the blood of the adult and nestling cliff swallows. The main parasite is the swallow bug, an avian bedbug. Larger colonies have more bedbugs, with some nests containing up to 2,600 parasites each. Close nesting contributes to the spread of the bugs, allowing these little miniature vampires to more easily find hosts to feed on. Early on, we studied the severity of the parasite infestations through fumigation experiments in which we used a dilute solution of insecticide on some nests, leaving others untouched. We found that nestlings reared in fumigated nests were much heavier, grew faster, and survived better, showing that the bugs were quite costly to the swallows. These costs were greater in large colonies, and it's our guess that parasitism by swallow bugs is the single worst disadvantage of group life for these birds.

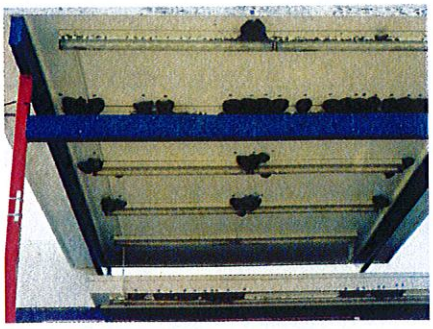
FLOCKING TOGETHER

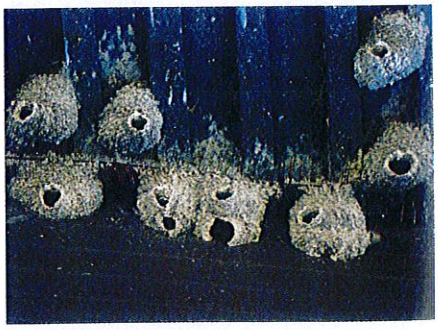
In contrast, the advantages of grouping have been more elusive. Eventually we discovered that cliff swallows primarily benefit by using each other to find food. Feeding on swarms of small insects that are unpredictable and change position often, the birds face the tough task of constantly relocating these moving restaurants.

The Israeli ecologist Amotz Zahavi proposed some years ago that one reason birds flocked together at particular places was so that individuals unsuccessful at feeding could follow knowledgeable hunters to food. Prior to our study, ornithologists had tried to determine if bird colonies worked this way, with largely equivocal results.

We discovered that cliff swallow colonies along the Platte River are indeed information centers, and as Zahavi proposed, birds unsuccessful at feeding would look to see who

Ever adaptable, swallows cling to habitats, both natural and man-made, in the most determined of ways. From left, under a gas station canopy, on a building, on the morning-glory at Lake McConaughy, on a cliff, under the eave of a barn. Above, a bullsnake begins a nutritional cycle at a swallow nest. Large photo, right: swallows gather mud—their bricks and mortar.



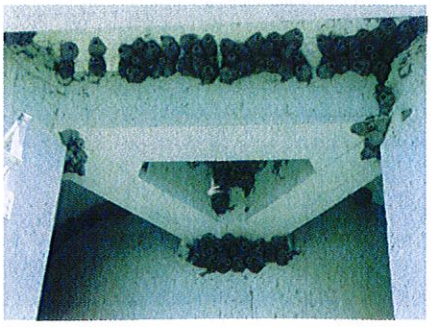


returned to their nests with mouths full of insects and follow them the next time they left their nests. Thus, birds in bigger colonies with more neighbors to watch get more food than birds in smaller colonies.

More recently, our research has shifted from describing the costs and benefits of colonial living to seeing how those costs and benefits influence the birds' survival and lifetime output of offspring. The criterion for evolutionary success is the number of young an organism produces over its lifetime: those producing the most young to reach reproductive age are the most successful. Thus, it is important to know how many offspring are raised each year, and how long an animal lives to produce those annual quotas.

HANDLING WITH CARE

To study this in cliff swallows, in 1990 Mary and I started banding large numbers of birds, allowing us to follow the same individuals over time. The birds are caught in mist nets made of fine-thread mesh that are supposed to be so hard to see that they look just like mist. We string the nets across the entrances to highway culverts or along



the sides of bridges where the birds nest, and the swallows get caught going to and from their nests. Each bird gets an aluminum band—a bracelet—around its right leg, and each has a unique number. When we recapture that bird in a later year, we have information on longevity, movement and the choice of colony that the individual has made. Cliff swallows are incredibly tolerant of being netted and handled, and they hardly seem to mind the interference and disturbance we cause.

With the help of two or three undergraduate assistants, we spend every day during May, June and most of July visiting different cliff swallow colony sites from Oshkosh to Maxwell. We band all the new birds we catch, but our principal focus is on recapturing birds banded in earlier years. Many swallows live five or six years, and a few have reached eleven years of age. We've banded more than 101,000 cliff swallows since the project started; we are not aware of any other study on birds with that many banded individuals.

DARWIN IN THE WILD

As Kara and I started the grisly task of picking up the corpses, I noticed that some of the dead birds were banded. This bridge was too tall to net, and we'd never banded any birds there. Apparently, these banded ones were swallows that immigrated to this colony from elsewhere.

That evening back at the lab, Mary and I sorted through a pile of at least 700 dead cliff swallows. I was sick to find some banded birds that were ten years old. These animals had made ten round-trips of 6,000 or so miles each between Nebraska and Argentina, only to be snuffed out by some cold weather that happened to last two days longer than normal. Many old friends lay dead in front of me on the table. It was some sort of excessive, horrendous nightmare I couldn't wake up from.

It took another day or two before I realized that all was not lost. Although at least 30,000 birds in our study area had died, about half the population survived. As I fought through my grief over the destruction of so many of "our" cliff swallows, I began to wonder why some survived while others did not. I saw that we had a wonderful opportunity to measure natural selection in action.

Bedbugs bite.
An engorged bedbug clings to the side of its frail host's neck. Blood-suckers, the bugs can cause markedly slower growth in affected populations, giving natural selection a toehold. At lower left, author and researcher Charles Brown makes communion with the swallows in a western Platte Valley drainage tunnel.

Natural selection, the central tenet of modern biology first espoused by Charles Darwin, refers to the process whereby certain individuals leave more descendants than others and eventually come to predominate in the population, replacing the less successful individuals. Selection can occur because some individuals reproduce better or because some individuals die, forfeiting any further chance to reproduce. Yet selection is hard to see in the wild; it usually occurs through small, accumulated differences in reproductive success over time that take several generations to become apparent. Consequently, contemporary studies that have shown natural selection in long-lived organisms are rare.

In 1899, a study often held up as an example of natural selection in action was done by Hermon Bumpus at Brown University. A severe ice storm killed several hundred house sparrows, and Bumpus picked up some of the dead and moribund birds. The ones that revived after being brought inside were considered survivors, and Bumpus compared skeletal measurements of these birds to the dead ones. He found that the survivors tended to be bigger birds overall but had shorter wings and tails. Overnight, the house sparrow population had apparently evolved toward greater size through selective mortality of the smaller birds. Could we have seen a similar effect among cliff swallows?

As the weather improved in the days immediately following the kill, we resumed our netting at the now much smaller colonies. Mary began measuring the wings, tails, legs, and bills of the surviving birds, measurements we had not been routinely taking up to that time. During the next nine days, she measured more than 1,000 survivors. When we returned to Tulsa with more than 1,800 frozen corpses, she took the same measurements on this sample of nonsurvivors. We were astounded at what we found: just as in Bumpus' house sparrows, this cliff swallow population had undergone major evolution during the six-day cold spell. Survivors were bigger birds with shorter wings and tails. The change in average size was much greater than in the house sparrows. We had witnessed evolution.

We also discovered differences in the degree of bilateral symmetry among survivors and nonsurvivors. Most organisms have distinct right and left sides, and bilateral traits such as arm and leg length tend to be roughly equivalent on each side. But usually there are slight differences—asymmetry—between the sides if one measures carefully enough.

Some biologists now believe that symmetry reflects an individual's overall health and vigor; an animal with right and left legs the same length is probably a better quality organism than one with a right leg longer than the left. Increasing evidence indicates that some animals, including humans, may assess the degree of bilateral symmetry when choosing mates and tend to select the most symmetrical ones. Symmetry in wing and tail was apparently important for cliff swallows during this bad weather: survivors had highly symmetric wings and tails, whereas the dead tended to have right and left sides that matched less well. High levels of symmetry were selected, and the population suddenly became one of more symmetric individuals.

Our results provided some support for the view that symmetry might be a good criterion to use for picking a mate. A female selecting a symmetric male may pass on the traits that will enable her offspring to survive periods of bad weather. We think symmetry is advantageous during cold snaps by allowing the birds to fly more efficiently, and these slight aerodynamic benefits may make the difference between life and death when weather conditions are marginal.

As we began to look at the mortality patterns more closely, we also found that individuals that lived tended to be younger birds. We had expected the reverse, assuming that older swallows might be more experienced and know where to go to find food when times were tough. Instead, it appears that the older birds were farther into nesting and had depleted more of their fat reserves, making them more vulnerable to starvation. If you're a cliff swallow along the Platte River in May, it's clearly best to be young, big and fat.

It now appears that body size in cliff swallows may be particularly sensitive to unusual climatic events. The 1996 period was certainly unusual: We looked at the climate records for North Platte extending back to 1875, and found only one similar period that likely affected the swallows in the same way. Since that one was in 1967, this cliff swallow population may have undergone relatively recent change in body size. We had never before appreciated how important body dimensions in cliff swallows may be. Now, we take morphological measurements on as many birds as possible.

Two field seasons have now passed since the great cliff swallow kill of '96. The population has increased each summer, but it is still below the pre-kill level. Although those trash bags full of dead birds with bands will haunt me the rest of my life, I'm also excited at the prospect of watching the population recover and seeing whether these evolutionary changes are permanent. There will be much more to learn from the cliff swallows of the Platte River Valley in the next seventeen years.

Charles R. Brown is associate professor of biology at the University of Tulsa. His most recent book, *Swallow Summer* (University of Nebraska Press, 1998), is a chronicle of the (prekill) 1995 field season, written for nonscientists.