

# The Great Egg Scramble

*In a cliff swallow colony, eggs tend to travel*

by Charles R. Brown and Mary Bomberger Brown

May 16, 1987, 2 P.M. A road culvert just below Lake McConaughy, Nebraska, containing 1,100 cliff swallow nests. We had settled into what looked like another routine afternoon of watching swallows at their nests. The day was sunny and hot, with not a hint of a breeze; we would have to concentrate just to avoid falling asleep in our lawn chairs. Suddenly, White-Black-White appeared in the small entrance hole of her nest carrying a grape-sized white object in her bill. Hardly pausing, she flew to a neighbor's nest, entered it, and within seconds reappeared without her white cargo. She briefly peered out of the nest, then casually flew back to her own. We had spent almost two years trying to witness just such an event: a cliff swallow moving an egg from one nest to another. We had long been aware that cliff swallows furtively lay eggs in other cliff swallows' nests—a practice known as brood parasitism—but actual egg transfer, as demonstrated by White-Black-White, was a phenomenon that we had only guessed at.

The most famous brood parasites, the European cuckoo and the brown-headed cowbird, lay their eggs in nests of other species. Cowbirds parasitize dozens of species of North American birds. Only within the last five years or so has brood parasitism among individuals of the same species been recognized as a fairly common tactic of breeding birds. The highly colonial cliff swallow of the American West may well be its major practitioner. Living in dense colonies, a female cliff swallow usually has plenty of opportunities to parasitize her neighbors, either by the classic technique of quickly laying an egg in an unattended nest or by transferring an egg she has already laid to another nest. This behavior, particularly the transfer of eggs, has been the focus of much of our research in the Nebraska Sandhills near Ogallala. Since 1982, we have located and studied, to varying degrees, 340 cliff swallow colonies.

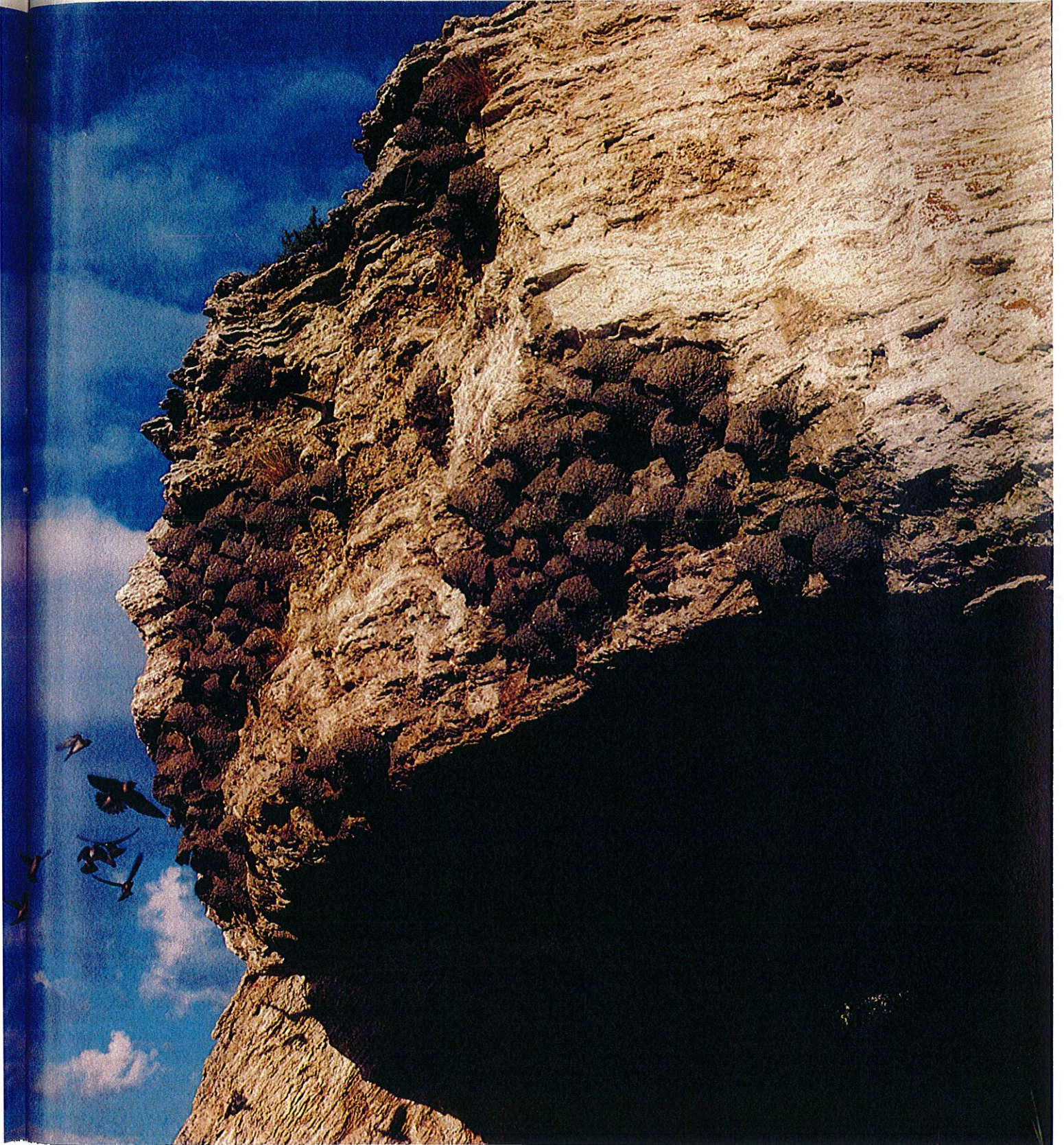
Cliff swallows build their gourd-shaped mud nests beneath rocky overhangs on the sides of steep cliffs and canyons. In recent times, however, the birds have discovered that artificial structures offer safer places





*Cliff swallows return to their cliffside nests. Many of these highly social birds now nest on bridges and in culverts.*

Tom Mangelsen







for nests. Any bridge or highway culvert that has a rough vertical surface for nest attachment and a protective overhanging ledge is prime nesting habitat for cliff swallows. The birds have thereby expanded their range eastward across the Great Plains, following major prairie rivers that are spanned by bridges and are close to culverts under highways. In our study area, most colonies are found along the Platte River, including those in ancestral nesting sites on the North Platte River or along the shore of Lake McConaughy, Nebraska's largest lake.

One of the most social species of North American birds, cliff swallows reside in colonies containing as many as 3,500 nests, although in Nebraska, colonies with as few as five nests can be found within several miles of the largest. Cliff swallows do almost everything as a group. They

forage, gather mud for their nests, preen, and migrate together and most likely spend winters in Argentina in large flocks. Known for their legendary return to the mission of San Juan Capistrano in California on the same day each year, the swallows reach the United States in March and spread to most parts of their breeding range by early to mid-May.

When the birds arrive in our study area, they immediately begin to investigate potential nest sites. The mud nests can remain intact for years, so some of the more protected sites contain usable nests at the start of the breeding season. Competition for these nests is intense; securing one saves a bird up to two weeks of construction time and allows it to begin egg laying and chick rearing relatively early in the season. Such a head start not only increases the bird's chances of successfully

sneaking an egg into a neighbor's nest but also enables the swallow and its vulnerable young to avoid extreme infestations of insects, primarily swallow bugs, that inhabit nests and whose numbers increase as the summer wears on. These unwelcome tenants carry disease and sap the strength of nestlings by sucking their blood.

Able to fast for years in unoccupied nests, swallow bugs quickly spread from nest to nest in summer by riding on feathers or crawling along the surface of the cliff or culvert. They exact a heavy toll, causing almost half of all nestling deaths. When scouting out possible nest sites in spring, cliff swallows avoid old nests that remain heavily infested, and in some cases, the birds abandon former colonies completely.

As soon as we began our research, we found signs of brood parasitism. Birds can



*In May, cliff swallows, below, gather mud for nest building. They take about two weeks to construct nests, which are plastered to a rock wall, left, and crammed together. In their haste to breed, some swallows lay eggs before the nests are complete.*

George D. Lepp



up to twelve days after the resident had started incubating, but still hatched at the same time as the clutch to which it had been added. This could only mean that the egg had been incubated elsewhere before being placed in its foster nest.

Most of our colony watching was carried out at a small road culvert near the University of Nebraska's Cedar Point Biological Station. Because we needed to identify individuals, we caught cliff swallows in mist nets strung across the culvert's two entrances and used marking pens to flag the birds' striking white forehead patches with unique two- and three-color combinations. During many hours of sitting just outside the culvert, we discovered that birds that lay eggs in other nests also maintain a nest of their own within the colony. In most cases, a female slips an egg into a nest nearby, seldom traveling farther than about five nests away. Brood parasitism is tricky. Nests can rarely be invaded if a neighbor is home; thus, potential brood parasites are always on the lookout for an unattended nest and constantly attempt to enter nearby nests, darting from their own to a neighbor's and back. If a nest owner is entrenched, it immediately lunges and repels the trespasser. If a parasite does find a momentarily unguarded

nest, she can lay her egg and be gone in a little as ten seconds.

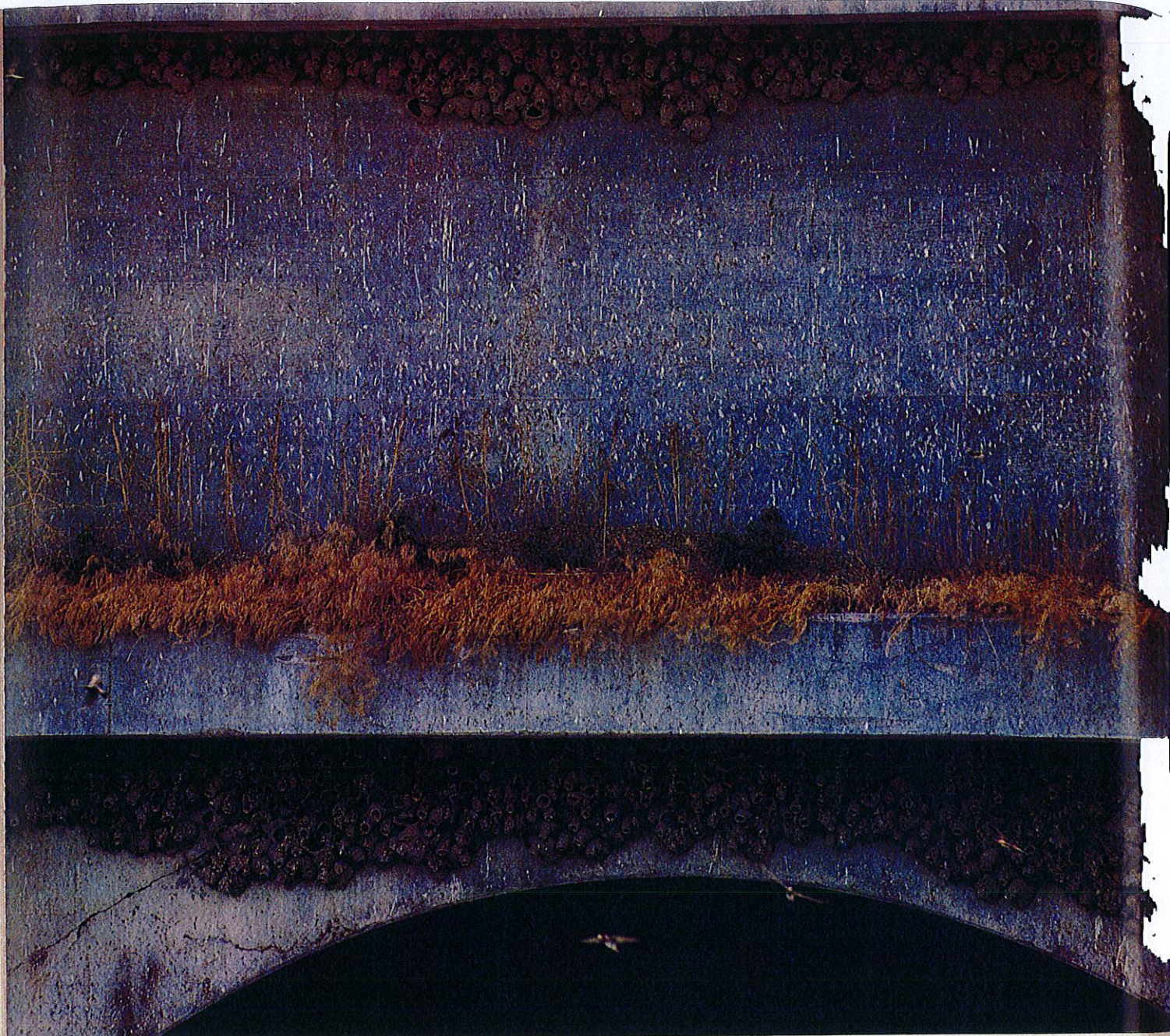
Males of many colonial bird species escort their mates whenever the females leave the colony. This behavior presumably helps a male insure his paternity by preventing rivals from copulating with the female. But a male cliff swallow guards its nest rather than its mate. The great risk of having its nest parasitized apparently leads a male cliff swallow to accept the lesser risk of cuckoldry if his mate wanders away unescorted. As a result, male and female cliff swallows take turns staying at the nest during its construction and during egg laying and incubation. Only when this arrangement breaks down (for unknown reasons) and the nest is briefly left vacant can alien eggs be deposited or transferred.

The average cliff swallow clutch consists of four eggs laid on consecutive days. The host recognizes and discards an alien egg only when it appears in her nest five or more days in advance of her own laying. If an alien egg is deposited within three days of the host's starting her own clutch, it will be accepted and incubated. The invading bird seems able to sense the imminent onset of laying by potential hosts. From the parasite's standpoint, early laying in a

lay only one egg per day, so the appearance of more than one in a nest during a twenty-four-hour period told us that a female or females other than the nest owner had deposited eggs there. Extrapolating from these data, we estimated that at least 10 percent of all the nests contained alien eggs. This method, however, provided no clue as to who was parasitizing whom. We wondered whether the strange eggs were laid by wandering, nestless birds, by birds whose nests had been suddenly destroyed, or by other colony members that had nests of their own. To find out, we embarked on an intensive program to determine which individual swallows were responsible for laying the parasitic eggs and how frequently they did so.

Up to that point, evidence that some cliff swallows moved eggs was indirect. At times, an egg appeared in a particular nest





host's nest increases the likelihood that its parasitic egg will be among the first to hatch, and this, in turn, enhances the nestling's chance of survival. Even when the host has already started laying, the parasitic egg is usually deposited early within this period. Cliff swallows that lay smaller clutches than average tend to be most often victimized by their neighbors. Perhaps the parasite seeks out nests owned by birds that are less fecund, thus insuring less competition later from the host's own young. Or perhaps the host reduces its own output of eggs and adjusts the clutch to a normal size when it notices an extra egg in its nest.

Most parasitic eggs hatch, and nests containing such eggs result in more healthy fledglings, on average, than cliff swallow nests in general. Given this payoff, one might expect parasitism to be

rampant within swallow colonies; it apparently is controlled only by the difficulty of finding a vacant host nest. But parasites themselves must also pay a price. We discovered that well over half of all parasitic birds were in turn parasitized by others during brief absences from their nests. Parasites end up caring for virtually the same number of young as do their victims. The action at a colony resembles a game of musical chairs, with everyone dashing into the nearest empty seat.

We wanted to know whether large colonies meant more brood parasitism. Because there are more nests to lay eggs in, breeding in a sizable colony could be a decided advantage to potential parasites and a disadvantage to hosts. We found that in the smallest cliff swallow colonies in Nebraska, those with ten or fewer nests, brood parasitism occurs rarely, if at all.

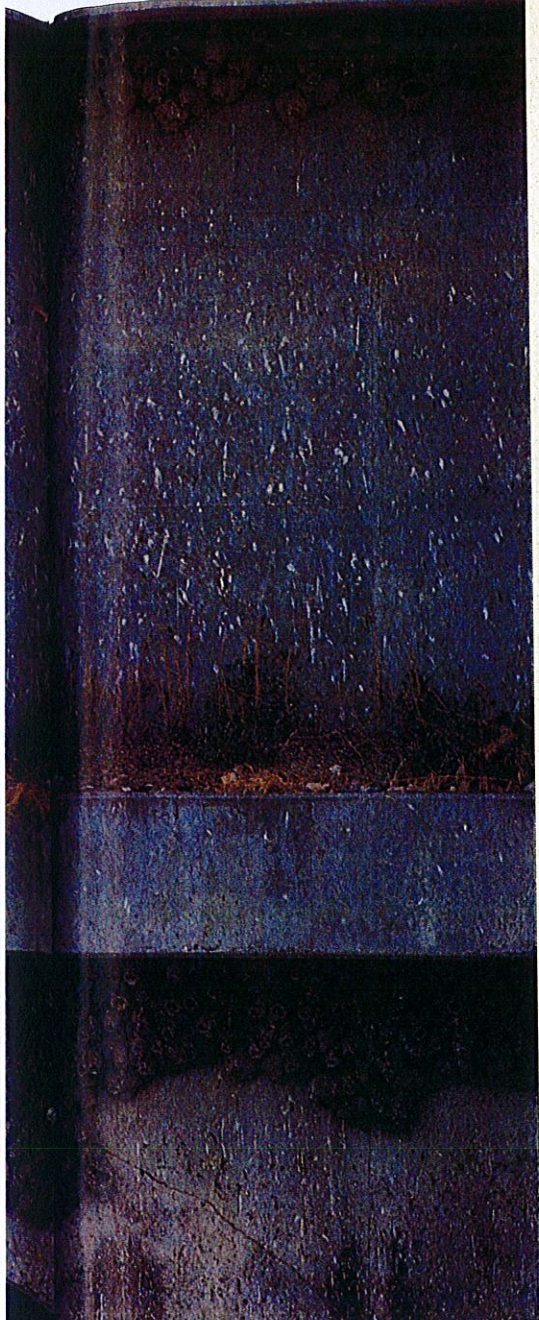
Birds in tiny colonies seldom even attempt to interact. In larger colonies, however, we estimate, based on our observations and genetic data, that at least 22 percent of nests, and probably as many as 43 percent, contain at least one alien egg.

What benefit might this practice hold for cliff swallows? If a swallow does not put all its eggs "in one basket," the odds are better that at least one of its young will survive. In the natural nesting habitat of rocky cliffs and canyons, nests are often destroyed by rock slides and inclement weather. In many cases some nests remain unscathed, but it may be difficult to predict which sites are the most vulnerable. Spreading the eggs around makes sense for a highly seasonal breeder such as the cliff swallow, which typically raises only one brood and has a relatively brief, eight-week breeding season with few chances to



*The side of a concrete spillway at Kingsley Dam on Lake McConaughy in Nebraska, left, offers ideal nesting conditions for cliff swallows. Three thousand pairs nest at this site. Swallow bugs clustering at the lip of an unoccupied nest, below, wait until a bird enters or even brushes against the nest, then crawl into its feathers. A single nest can contain up to 2,500 of these blood-sucking insects, which account for nearly half of all nestling deaths.*

Both photographs by Art Gingert



renest. In addition, some nests become heavily infested with swallow bugs during the course of the summer, while others remain relatively insect free. Distributing eggs increases the chances that some offspring will hatch in uninfested nests.

Our colony watch revealed another surprising facet of cliff swallow social behavior. Besides laying and moving eggs into nearby nests, these birds also destroy some of their neighbors' eggs. We had suspected that some kind of hanky-panky was going on when we noticed that nests would at times mysteriously lose one out of a clutch of eggs. Without evidence of other predators, we could only blame other cliff swallows.

Egg destruction, it turns out, is carried out almost exclusively by males. Birds search for unattended nests, usually within five nests of their own. After gain-

ing access, they flick one of the eggs with their bill and roll it out the nest opening, or they occasionally spear an egg with their bill and drop it into the water underneath the nests. We repeatedly observed birds doing away with just one egg, despite the opportunity to get rid of others as well. Orange-Pink-White was a particularly fiendish male. We saw him enter three neighboring nests and relieve each of them of an egg. On Orange-Pink-White's fourth raid, the resident bird returned and kicked him out after he had rolled an egg almost up to the nest opening.

Like brood parasites, egg destroyers are selective. The birds that have average or larger than average clutches bear the brunt of the losses. Perhaps the most fecund females are more vulnerable because they must leave their nests more often to forage and replenish their energy after the physical drain of laying a large clutch. The net effect is a near equalization of the clutch sizes of all the birds.

A few nest owners, for unknown reasons, just seemed to be inept, leaving their nests unattended more often. Yellow-Orange and his mate could never coordinate the guarding of their nest. They had, we think, at least three alien eggs laid in their nest and three eggs tossed out. Who knows

whether any of the nestlings this pair raised were in fact their own.

Some egg destroyers wait until a general alarm call is given at the colony before making their move. Sounded in response to a passing predator, such as an American kestrel or a bullsnake, alarm calls induce many, but not all, of the swallows to flush momentarily from their nests. We observed five instances of egg destruction and one of parasitic laying during alarms. While we have not determined which birds actually give the calls, we do know that they are sometimes sounded when no predator is in sight and that some individuals fail to react to the warning. Could the perpetrators themselves be crying wolf to fool their neighbors into leaving their nests?

The obvious explanation for egg destruction is that it reduces a neighbor's clutch by one egg so that a parasitic egg may then be added. (Cuckoos and cowbirds often remove one of the host's eggs before making a deposit.) We saw only one instance of such substitution, which was notable also because it involved a female. On one morning in mid-May, we saw Blue-Black-Blue enter an unguarded nest near her own. She immediately tossed out a single egg that the owner had laid



that day, retreated into the interior, laid her own, and quickly returned home. All the other cases of egg destruction we observed were perpetrated by males.

Why do males, in particular, destroy their neighbors' eggs? One possible answer is that removal of an egg causes a female to continue laying until she produces a surviving clutch of some fixed size. As long as a female is laying eggs she remains sexually receptive. Male cliff swallows, which take every opportunity to copulate with neighboring females, have a stake in those birds' sexual receptivity. Destroying some of their eggs may be a way of maintaining it.

Another possibility is that egg destruction is a prelude to egg transfer. Nests that had eggs destroyed were more than three times more likely than others to later have an egg moved into them. This suggests that several days after they have removed an egg—if they again find the nest unattended—birds slip in a transfer. By removing an egg beforehand, a parasite reduces the competition between nestlings when the eggs hatch. Perhaps both members of a pair are actively involved in brood parasitism: the male removes host eggs, the female delivers her own.

Our picture of life in a cliff swallow colony is one of considerable and near constant strife. Even before the first egg is laid, the birds are vigorously undermining their neighbors by stealing nest materials, such as grass and bits of mud. We once watched a male repeatedly ransack a neighbor's nest, making ten trips in less than fifteen minutes to pilfer grass used to line the nest. He completely emptied his neighbor's nest of all grass and furnished his own lavishly. Why would a bird risk getting its tail kicked, literally, by snatching an abundant commodity he could easily collect directly from a nearby pasture? Such thievery may allow a swallow to keep a close watch on his own nest and prevent his neighbor from turning the tables. It also reduces the thief's chances of falling prey to common grackles, larger birds that sometimes attack, kill, and eat cliff swallows that alight on the ground to collect grass stems.

By early to mid-June, at the end of the

*An adult swallow that has found a swarm of flying insects returns to its nest, its throat bulging, to feed a gaping chick, below. Other swallows from the colony follow successful foragers to learn the whereabouts of insect swarms. Nests tucked precariously between rock crevices, right, may be washed away by heavy summer rains.*

Art Gingert



laying period, the frantic "dog eat dog" atmosphere of the cliff swallow colony subsides, the birds put their energy into feeding their demanding chicks, and the reason that they live in colonies becomes clear. Swarms of insects, brought temporarily together by convection currents or forming after a mass hatching of larvae, are rich sources of food for the Nebraska swallows, but finding swarms is often a matter of luck. A swallow that is unsuccessful in locating a swarm returns to its nest and observes its neighbors. Swallows that have encountered a swarm uninten-

tionally signal their good fortune by their bulging throats and the insects protruding from their full bills when they return to feed their young. The hungry bird will follow the successful one on its next foraging trip and feed on the temporary abundance of insects. Individuals that are followers one day may find food and become guides the next, so all the birds benefit. The same neighbors that were enemies earlier in the season are now vitally important to each other. For the rest of the summer, at least, cliff swallows look almost like good neighbors. □



