Cliff swallows are at home on the sides of cliffs and, increasingly, on highway overpasses, bridges and culverts. CHARLES R. BROWN

BUILDING A BETTER SWALLOW

As mankind restructures the landscape, one species changes with it.

STORY BY Conor Gearin

THE 123-YEAR STORM

Evolution can happen any day, any time. Sometimes all it takes is a particularly nasty Midwestern rainstorm.

In late May 1996, two Ford F-150s rolled toward a roadway culvert in the flat plains of southwestern Nebraska. Rain streaked the

windows as the biologists inside peered out with binoculars. Attached to the underside of the culvert were gourd-shaped nests made of mud and straw. Some birds fluttered around the nest, but many others sheltered inside. They might not have looked like it at first, but they were all starving to death.

A fierce six-day storm was keeping the cliff swallows from catching enough flying insects, their only food source. The biologists didn't dare get out and walk closer, because that would flush the swallows from their nests, causing them to lose more of the energy stores keeping them alive. Dead swallows lay in the mud under the culvert.

For the scientists, it was a rough moment in a long relationship with the swallows. Biologists Charles Brown of the University of Tulsa, Mary Bomberger Brown of the University of Nebraska-Lincoln and their teams of students had been watching, catching, and measuring cliff swallows around Ogallala, Nebraska for 14 years.

Cliff swallows (*Petrochelidon pyrrhonota*) are small songbirds with dark wings, a chestnut-colored throat, a blue back, an orange rump and a white forehead patch. They live in large colonies of up to 6,000 nests densely clustered together. In 1815, John J. Audubon dubbed them the "republican" swallow after seeing the complex societies they form to raise their young.

Audubon first found the species nesting on natural rocky outcroppings. He was surprised a few years late to encounter them again living on the sides of houses near Cincinnati. In the 20th century, the species began colonizing highway overpasses, bridges and culverts in Midwestern farmland. These features became more common as people built up the network of roads and infrastructure needed to ship goods on trucks and maintain large farms. It was a winning scenario for cliff swallows, who spread their colonies across the transformed landscape.

Because of their lifestyle, the species is ideal for studying how social systems have evolved in animal populations in general. Brown and Bomberger Brown, who were married for a time, have now studied the Ogallala cliff swallows for 35 years and continue to co-write papers on them. While they began by asking how the swallows evolved over the millennia to their current state, those rainy days in 1996 made them wonder if the birds were changing into new forms right in front of them.

The scientists knew it had rained that long only twice in the past 123 years, and overnight frost didn't help. They also knew how sensitive the swallows were to storms that kept them from catching insects on the wing. "I always sort of live in fear of these events during the first half of the field season because you can lose a lot of your study animals," Brown said. The birds could usually go without food for the typical two- or three-day spring rainstorms. This one was different. "When it got to four days, I started to get worried," he said. "When it reached six days, I knew we were seeing something that was very unusual."

When they weren't watching the colonies from a safe distance, the biologists contemplated the situation from the dining lodge and cabins of the Cedar Point Biological Station. They wondered how many adult birds they were losing, how many nests they could no longer study. From the station's windows, they looked out over Lake Ogallala, which lies below a dam across the North Platte River. They saw birds trying to fly out over the lake, hunting desperately for any insects still they could find in the rain.

On the seventh day, after the storm subsided, they saw the grotesque results. Swallow corpses lined the lakeshore like a bathtub ring.

The scientists pulled on their boots to survey the casualties and collect as many as they could. If they couldn't study the birds alive, they'd have to learn what they could after death. They found dozens under the road bridges where the birds nested. Many more starved inside the nests. Brown surmised that others fell into Lake Ogallala and were lost to science. In the end, they estimated that 53 percent of the population had been wiped out, leaving nearly half the nests empty. Looking at the metal ID bands on the birds' legs, they realized they were collecting "old friends," individual birds they had known for up to 10 years, Bomberger Brown said.

The die-off became a different kind of bounty for the scientists. Death is one of evolution's favorite sculpting tools, and that spring in Ogallala, death was everywhere.

Cliff swallows return to Nebraska earlier now than 30 years ago. This allows them to start their colonies when it's cooler, wetter and there are less parasites, but also exposes them to spring storms. JOEL G. JORGENSEN

Bomberger Brown bands a cliff swallow. A team of biologists had been researching the species for 14 years before hundreds died in a 1996 storm. CHARLES R. BROWN

This catastrophe got them thinking — did the birds that died in the storm have different traits than the survivors? The biologists planned out a careful autopsy. For that, they needed a new piece of equipment: a mass sarcophagus for cliff swallows. A maintenance worker at the field station soon hammered out a large cedar chest, putting in insulation boards to keep its contents cold. More than 1,800 cold bird bodies went into the box. They also needed a snapshot of what the group of survivors looked like. Near the colonies, the team put up thin mesh nets between two poles, catching over 1,000 survivors and measuring them.

Bomberger Brown, skilled in using taxidermy to prepare museum specimens, thawed the cliff swallows in the box and measured the wings, tails, lower legs, beaks, body length and mass of each one. Including the surviving swallows they netted, she and the team measured 2,866 birds. She found that the survivors had larger bodies on average than the birds that died. The larger body sizes probably allowed those swallows to store more fat and retain more body heat to survive the long storm. Their wings and tails also tended to be more symmetrical, making for more efficient flight.

Even more intriguingly, the surviving birds on average had shorter wing and tail feathers. This advantage is less immediately obvious, but Brown thought it wasn't an accident. Perhaps the sparse flying insects available during the bad weather were harder to catch and called for sharper turns than the swallows ordinarily needed to perform. Those cliff swallows with shorter wings and tails, which make for more acrobatic flight, were able to catch these insects. They had an advantage.

We often think of natural selection as happening slowly, in the distant past. But here, the cliff swallow team had documented it taking place rapidly and in real time. As the storm put pressure on the swallows, the shorter-winged ones had a better chance of surviving than the longer-winged ones. Because they survived, they could reproduce and pass on their genes. In other words, natural selection favored the shorter-winged swallows.

Like Darwin, the scientists had begun by asking how cliff swallows evolved to the way they are now — why and how they had developed their complex social structures and nesting colonies. But while working out this riddle, they watched evolution unfolding right before their eyes.

"We learned to see things differently, to see and think about things more broadly," Bomberger Brown said. "1996 was a watershed. It was a big deal."

Death is one of evolution's favorite sculpting tools, and that spring in Ogallala, death was everywhere.

EVOLVING IN THE DANGER ZONE

Later in the summer, the pickup truck with the cliff swallow field crew drove down a country road. Compared to the huge Nebraska sky, the truck had about the same puny scale as the wildflowers and the birds. But they halted to collect one small dot in that landscape, one data point: a dead swallow on the side of the road.

Brown makes a point of picking up every single dead bird of any species the team comes across, said Amy Moore, who has worked with him for more than 10 years. And they certainly stop the car every time someone spots a dead swallow.

Cliff swallows nesting along rural highways live in the danger zone. They push their flight abilities to the limit every day of the breeding season. Often they stand on the asphalt until a car comes and then try to escape at the last minute. The results are dead swallows on the roadsides every year — the ones that couldn't pull up fast enough to dodge a windshield. The team scoured the same roads year after year, keeping their search efforts consistent over the decades. They ended up with 104 dead birds in all, but they felt they had seen less roadkill in recent years.

They also kept dead swallows they had accidentally killed during research. Sometimes while catching birds with nets, some swallows had "little bird heart attacks" or died for other reasons, Bomberger Brown said. The researchers made the best of these situations and preserved each bird. They collected 134 such birds.

These two groups of birds made for a useful comparison. The birds that died in the nets essentially died at random, not because of any particular trait. That meant they were probably a good representation of the population at large. As a double-check, the team compared whether the measurements of the birds that died during netting were any different than their measurements of birds that survived netting. They were the same.

Looking back at three decades of specimens, the researchers confirmed their hunch that they had collected fewer road-killed birds each year. Of their 104 road-killed birds, most of them came from the early years, when they found about 20 birds per year. The number fell to around 10 per year in the late 1990s, to only two to four in recent years. And over the same period, the local population of cliff swallows nearly doubled, so it wasn't just that there were fewer swallows around to get hit.

Brown wondered if there might be something behind the decrease in roadkill. Rather than getting smarter, maybe the birds' bodies were changing.

When Brown first asked Moore to start crunching numbers on the 30-year dataset, she was skeptical they'd find any meaningful trend. Though people drive pretty fast on the country roads around Ogallala, Moore figured there just wasn't a high enough volume of traffic to force natural selection in only three decades.

But when they graphed the length of the swallows' wings over the years, they found something extraordinary. The general population of swallows' wings had decreased in length fairly smoothly over 30 years, falling from nearly 111 millimeters to 106. Meanwhile, the road-killed birds tended to have wings over 109 millimeters. This 4-millimeter change might seem negligible, but small changes in wing shape can have strong effects on flight physics. The researchers already knew from the earlier study about the effect of the storm that shorter wings tend to help swallows maneuver more sharply.

"We've always sort of laughed that cliff swallows and cockroaches will inherit the earth," Bomberger Brown said.

While this finding was exciting, the work had just begun. The team had many alternative explanations to rule out, each one requiring a search for the right facts. Could the population of mammal scavengers have increased, taking away more birds before the team could find them? While they didn't have information on the Ogallala population of scavengers, they knew that skunk numbers in all of Nebraska had fallen, so that explanation was unlikely. They also ruled out changes in traffic and made sure they had surveyed the same lengths of road each year.

After going through all of these ideas, Brown and Bomberger Brown felt confident in concluding that natural selection influenced the swallows' wing length. This characteristic was so beneficial that it came to dominate the population fairly quickly.

In evolutionary terms, this is a rapid shift, happening in the space of a human generation rather than in geologic periods of thousands or millions of years. Brown and Bomberger Brown published a paper on this surprising outcome in *Current Biology* titled, "Where Has All the Roadkill Gone?"

Looking at classic examples of evolution such as orchids, natural selection looks like a process that makes a species ever more graceful. In the coevolutionary partnership between an orchid and the butterfly species that feeds on it, the flower's long tapering opening and the insect's perfectly matched unrolling proboscis became more elegant and specialized with time.

With the cliff swallows, evolution wasn't a matter of grace. The ancestral cliff swallows started off more like stealth bombers with long, narrow wings. With the arrival of country roads, SUVs and 70-mile-per-hour speed limits, they needed a different design. Natural selection sculpted them into a new form, just not necessarily a more beautiful one. What we got, Bomberger Brown said, was basically the crop-duster model of a cliff swallow. The wings got stubbier, the flight more daredevil.

But there's a potential downside to this swallow tune-up. Every winter, that crop duster has to fly all the way to South America. Cliff swallows are long-distance migrants, spending their winters along the Rio Paraña, a grassland river much like Nebraska's Platte River, near the borders of Argentina, Uruguay and Paraguay. Once natural selection tricked out the population with barnstorming wings, they might have just lost energy halfway to the wintering grounds.

Fortunately, even with the shorter wings, the swallows have continued to leave Nebraska in the fall and return from South America in the spring, traveling thousands of miles. For now, their wings let them handle both the challenge of migration and the challenge of car-dodging. It's a balancing act, but they seem to have landed in an evolutionary sweet spot.

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This adds to a precious handful of examples of rapid evolution that scientists have been able to document in birds. In fact, it's so rare to witness such changes that the best-known example required a return to the birthplace of evolutionary theory: the Galapagos Islands. Peter and Rosemary Grant of Princeton University have studied Darwin's finches since the 1970s and watched the birds' beak and body sizes shift in response to changes in their food supplies.

There's one caveat to make — ideally, you'd want an experiment to really demonstrate that a species recently evolved. Differences in traits can show up in populations that aren't the result of shifts in genetics. For example, a pine tree growing at the top of a mountain replaces its needles less frequently than one growing in the valley to cope with the lower humidity at high elevations. In that way, trees with the same genes could look very different. An experiment called a "common garden" lets you sort out whether such a change is genetic.

In this test, scientists move some individuals from the changed population and some from the unchanged population and raise them side by side in an environment that's between the two extremes. With the pine trees, you'd raise them in middling elevations. With cliff swallows, perhaps you'd raise them somewhere with a medium amount of traffic. If the change isn't genetic, the offspring from the two populations would look more like each other over time. If it is genetic, they'd retain their differences through many generations.

This kind of test is challenging with wild

Compared to the huge Nebraska sky, the truck had about the same puny scale as the wildflowers and the birds. But they halted to collect one small dot in that landscape, one data point: a dead swallow on the side of the road.

birds, though. Brett Sandercock, who studies grassland birds at Kansas State University, says songbirds wouldn't hang around in a common garden. "You pick up a white-crowned sparrow in Texas and take it to California — it can actually navigate and go back home," he said. For this reason, more work on evolution has been done with fish and plants. Both are much less prone to escape. Neither the Grants nor Darwin used an experiment with the Galapagos finches. As with the cliff swallow study, careful measurements of change and consistent differences had to suffice.

Sandercock also noted that while cliff swallows have adjusted well, the story is different for most other birds living in the Great Plains. This is especially true for ground-nesting grassland species. In the historic plains, there were almost no trees or shrubs around to use for a nest. Accordingly, many prairie songbirds like grasshopper sparrows and bobolinks, as well as gamebirds like prairie chickens, have always made nests within grassy cover and cannot adopt a different strategy. It would require an entirely different lifestyle, not just translating the same plan to a new situation, as with the cliff swallow. "If you convert [the land] to soybean or corn, that's it," said Sandercock. "It's not suitable."

THE FORECAST

There might be limits to how far the swallow lifestyle can be pushed. In 2014, Brown and Bomberger Brown looked back at how 30 years of a warming planet had affected their birds. The swallows have been arriving earlier and earlier in the spring over the years, and it's likely that climate change is the cause.

In western Nebraska, climate change means more and deeper droughts. Returning from Argentina earlier in the year seems to let the swallows start their colonies when it's still cool and their parasites aren't yet at full strength. But it also means they have to contend with the stormy late spring period — the same period that killed so many in 1996 — in order to breed when it's wet and there are plenty of flying insects to eat. Brown said it's unclear how serious these changes will be for the species in the long term.

On the other hand, the species has shown its potential for adapting — in amazingly short windows of time — to the pressures that humans put on them. "All I know for sure is that it will be interesting to watch and to try to understand their response," said Bomberger Brown.