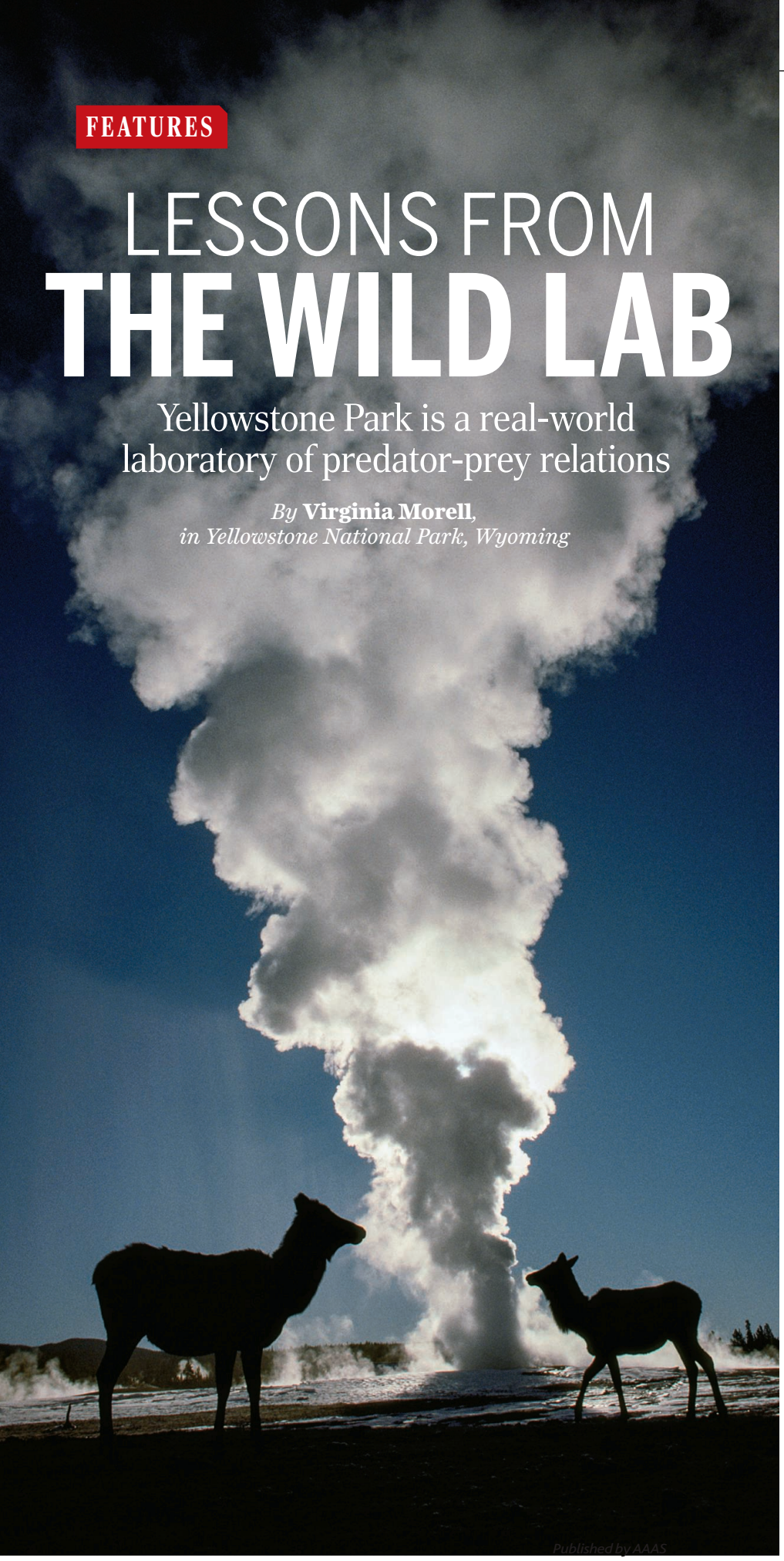
FEATURES

LESSONS FROM THE WILD LAB

Yellowstone Park is a real-world laboratory of predator-prey relations

By **Virginia Morell**,
in Yellowstone National Park, Wyoming



Yellowstone's elk, like this cow and calf near Old Faithful, face a changing ecosystem that includes wolves and cougars.

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Just before dawn on an icy January morning, Doug Smith skied off a main trail and headed toward a branch of Blacktail Deer Creek, pushing into thickets of willow, aspen, and wild rose. I followed, picking my way through the bare branches. They arched above our heads, and we didn't see the female moose until she burst from cover on the far side of the stream. She trotted smartly up a hill, then looked back to study us.

"That's a first," said Smith, a park wildlife biologist and the leader of its wolf, elk, and beaver projects. "I've never seen moose here. It used to be all elk." He stopped to show me where a nibbling moose, perhaps the cow we'd startled, had trimmed a few willows. "That kind of browsing is actually good for the willows; it stimulates new growth," he said. "Elk, though, eat willows almost to the ground."

He recalled riding along this same stretch of creek in the summer of 1995, when hundreds of elk browsed the banks. Their droppings littered the ground and the willows were mere stubs. "It's so different now."

Willows, aspen, cottonwood, and alders are beginning to flourish again along streams in Yellowstone's northern range, an area known for its elk herd. Biologists debate just why this shift has occurred. But many agree that a key factor is an animal we didn't see that morning, but whose presence we felt: the gray wolf.

Twenty years ago this month, not far from Blacktail Deer Creek, Smith and other park biologists set radio collars on six wolves, opened the door of their pen, and watched them bound away. Today, 95 Rocky Mountain gray wolves (*Canis lupus*) in 11 packs live in Yellowstone, hunting primarily elk, deer, and bison. The political controversy over the return of a feared predator continues, as does pressure to hunt them outside the park, but among ecologists there's little dissent: "Putting the wolves back was a bold and remarkable move," says Adrian Manning, an ecologist at the Australian National University in Canberra. "Nothing on this scale had been done before in restoration ecology."

The wolves' return set in motion a natural —and therefore uncontrolled—experiment that is still unfolding. "We were witnessing something that no one had seen before," Smith said. "Bringing the wolves back gave us an unprecedented opportunity to see how apex predators affect an ecosystem." With the reintroduction, Yellowstone be-

came only one of two places "in the lower 48 where you find the entire assemblage of large carnivores and ungulates that were present at the end of the Pleistocene," says Scott Creel, an ecologist at Montana State University (MSU), Bozeman, who has studied carnivores in the park and in Africa.

It's almost impossible to overestimate the park's influence on conservation decisions around the world, Manning adds. "We know the ecological theory and how the bits and pieces are supposed to work. But to see it happening as you can in Yellowstone is really quite remarkable."

One of Yellowstone's 11 wolf packs waits while grizzlies feed on the remains of an elk likely brought down by the wolves.

PHOTO: DANIEL STAHLER/NPS

Yet the wolves are only one of many such natural experiments playing out in Yellowstone, and some scientists are cautious about attributing all the park's recent changes solely to these carnivores. Since its founding in 1872, Yellowstone has been treated as something of a living laboratory, subject to shifting biases and ideas about how best to manage it. From shooting every last wolf to managing the bison like livestock, each intervention has had long-lasting consequences that scientists are still trying to understand and correct.

In recent years, biologists have gathered data on all of these perturbations and found clever ways to establish some controls and test hypotheses. Many think that the wolves triggered a cascade of changes in species from elk to coyotes to willows to bison to beavers. But other predators, including cougars and grizzly bears, may also be reshaping the ecosystem. Other scientists argue that climate change—drought, in particular—has been an equal or even greater partner in the transformation. And ecologists disagree over just how restored Yellowstone actually is.

Yet all concur that the restoration has taught important lessons, perhaps the most important being "there's no quick fix once an apex predator is gone," as Tom Hobbs, an ecologist at Colorado State University (CSU), Fort Collins, puts it. "Maintaining an intact ecosystem is so much easier than trying to restore it once the pieces have been lost."

MOST PEOPLE THINK OF YELLOWSTONE in its early days as a pristine wilderness barely touched by people. Nothing could be further from the truth. Archaeologists know that human hunters were in the park at least 11,000 years ago: Part of a Clovis projectile point made from Yellowstone obsidian was uncovered close to the park's north entrance in 1959, and an intact 10,000-year-old atlatl (spear-thrower) was discovered near the park 5 years ago.

By the time the first European-American trapper arrived in the early 1800s, at least a dozen groups of Native Americans were hunting the region's abundant wildlife. Herds of elk, pronghorn, bison, and mule deer roamed the northern range; cougars and bighorn sheep patrolled the rocky, mountainous interior; moose wandered the marshy meadows to the south; and grizzly bears ranged wherever they chose. The predator community of grizzly and black bears, wolves, coyotes, cougars, lynxes, bobcats, foxes, wolverines, and other, smaller species was intact, and it included humans.

Word soon spread about the area's beauty, wildlife, and hydrothermal wonders. In 1872, Congress set aside 8297 square kilometers for Yellowstone National Park, the first such park in the world—"the best idea America ever had," as writer Wallace Stegner once said.

The congressional act stated that "wanton destruction of the fish and game" should be prevented. But the young park's authorities had no means of enforcing these words. Many naturalists of the time loathed big predators because they killed "noble" game animals such as elk, and officials encouraged the killing of carnivores. Meanwhile, hunters shot so many thousands of ungulates as well as predators that one historian described the slaughter as an "ecological holocaust."

In less than a decade, wolves, cougars, and many smaller predators were largely gone from Yellowstone—a drastic culling whose consequences are still playing out. Grizzly bears (*Ursus arctos horribilis*) escaped this

On the hunt. An adult male wolf (*above, left*) leads the hunt on an older cow elk in Yellowstone. Such kills have curbed the elk population and prevented the ungulates from overbrowsing, allowing shrubs and trees to regrow. As a defense against wolves, elk now roam Yellowstone (*above, right*) in smaller bands.

fate because park visitors enjoyed seeing them. (In the 1930s, one hotel built an outdoor arena with bleachers so 1500 people could view the 50 or more bears snuffling among the garbage every night.)

In 1886, the U.S. Army was summoned to protect the park from poachers, and the soldiers also rid it of the last of the wolves and cougars. "Killing all these predators was the first natural experiment in the park," says William Ripple, an ecologist at Oregon State University (OSU), Corvallis. "The idea was to make Yellowstone a paradise for the elk."

As a result, for many decades, elk (*Cervus canadensis nelsoni*), vegetarian eating machines that both browse on shrubs and graze on grass, have been the "drivers of Yellowstone's ecosystem," Smith says. By the early 1930s, when every large predator except coyotes and bears was gone, the elk population stood at about 10,000 in the northern range. It was the largest elk herd in North America and another tourist attraction.

The abundant elk began cropping the park's vegetation, particularly the tasty woody plants along streams, causing severe erosion and leading to worries that they and other herbivores would starve. From the 1930s to the 1960s, park officials did everything they could to shrink the herd. Rangers and hunters shot and relocated elk by the tens of thousands. Some years they succeeded in reducing the numbers, but without continual culling, the animals bounced right back. "They just shot and shot elk; they shot left and right, and they pulled the carcasses out with Sno-Cats," Ripple says. "And still the vegetation could not come back."

This experiment ended in 1968, because Americans felt that shooting elk clashed with the growing idea of national parks as sanctuaries for wildlife. For the next 27 years, until 1995, the elk were left alone, neither fed by humans during the harshest winters as they once were, nor shot in the park. "Another experiment," Ripple says.

In the absence of predators, the elk rebounded, soaring to at least 19,000 in the northern range by 1994. The elk were running the park, but from an ecologist's viewpoint, they were running it right into the ground.

To reduce the numbers, Montana allowed elk that migrated outside the park to be hunted, first bull elk in fall and then also female elk, including pregnant ones, in winter. "Locals called it the 'meat locker hunt,' " Smith said, "because the success rate was so high." In 1995, the human hunt was upped so that hunters took about 9% of the elk population each year. That same year, the wolves were brought back. Yellowstone's ecosystem shifted yet again.

For starters, elk numbers plunged. By 2008, the northern range herd was down to just over 6000 animals—a drop of almost 70% from its peak. The combination of more wolves and fewer elk touched off a cascade of favorable effects, Smith and his colleagues say. Willows grew taller and stream banks greened, creating thickets where songbirds once again sang and nested. Bison and deer increased, filling niches reopened by the decline of elk. Today, in terms of biological richness, "Yellowstone is as good as it's ever been," says Smith, who details the changes in the most recent issue of the *Annual Review of Ecology, Evolution, and Systematics*. "Better even than it was in 1872."

Graphs of the numbers of wolf and elk in

PHOTOS: (LEFT TO RIGHT) DANIEL STAHLER/NPS; © DON JOHNSTON/ALL CANADA PHOTOS/CORBIS

Yellowstone's northern range now display a classic predator-prey correlation, similar to the iconic curve seen on Isle Royale in Michigan, where wolf and moose numbers cycled in tandem over decades, Smith says. As the wolves thinned the elk herds, their own numbers have suffered. In Yellowstone's northern range, wolf and elk populations are both down 60% from their peaks. "The decline in the elk has led to a decline in the wolves," explains MSU's Creel. "They're pretty tightly coupled."

Creel argues that wolf kills aren't the only factor driving the elk decline. "The other half is behavioral," he says. His research indicates that elk pregnancy rates have dropped by 20% to 40% across the park since the wolves were reintroduced. That's exactly the opposite of what you'd expect, as pregnancy rates typically go up when the overall population numbers fall, he explained in *PLOS ONE* last July. Yellowstone's elk may have changed when and where they feed to avoid the wolves. "They have to spend more time digging in the winter to begin to feed," he says, "and the quality of the food they are eating is lower. And that's all day every day."

The rise in predators has affected the elk's movements on the landscape, Smith agrees. At the Mammoth Hot Springs Terraces, a hydrothermal feature that in winter resembles an icy, tiered cake, about 20 elk, a mix of cows and calves, grazed on patches of brown grasses poking through a snowy crust when I visited in January. "We used to see groups of hundreds of elk here," Smith said. "Now, it's rare to see more than 15 to 20 together. We think that's because of the wolves; [smaller herds] may make the elk harder to find and hunt." (The wolves, though, are wise to their prey's tactics and have even slain the Mammoth elk on the steps of the nearby buildings.)

Creel's ideas are hotly debated. Some argue that the wolves were initially too scarce to have greatly influenced elk feeding patterns. Others say that indirect measures of elk pregnancy rates (as determined by a pregnancy-associated protein) do not reveal a decline. They also cite unpublished data that elk on the northern range, facing the park's densest wolf population, have a high pregnancy rate. Several scientists think the wolves have had only a minor effect on the elk and other species, arguing that drought and warmer winters have played more crucial roles.

Ecologist John Vucetich from Michigan Technological University in Houghton blames the meat locker hunt, which felled females in their prime, for the elk's dramatic decline between 1995 and 2005. "It's exactly what you'd predict," he says. Smith, too, thinks wolves are not the whole story. "We have to look at the full suite of predators—the cougars and grizzly bears, and smaller predators," he says. "And the human hunters."

WHILE ALL EYES were on the wolves, another predator stealthily reclaimed Yellowstone: cougars. No one knows when the first cats crept back. But in 1972, officials spotted a mother and two cubs. In 1995, the year the wolves were reintroduced, researchers estimated that 15 to 20 cougars were already making their home in Yellowstone.

"It's been a natural experiment," says park biologist, Dan Stahler, who oversees the park's cougar study, using two words I became accustomed to hearing. "No one paid very much attention to cougars at first," he says, "partly because they brought themselves back and partly because they're very quiet and secretive. They kill a lot of deer and elk, but we don't see them doing the killing. We don't hear them howling."

His team now tracks the cats from January to March, collecting scat and fur for

Highs and lows

Since Yellowstone's founding, animals have been removed, added, culled, or allowed to flourish.

1872
Founding of Yellowstone National Park

1886
Soldiers brought in to stop poaching

1902
21 bison in park's northern range (NR)

1907
Soldiers directed to kill predators; bears spared

1914
Elk numbers hit 35,000

1926
Last wolves and cougars in park eliminated

1936
Predator killing ends; coyotes protected

1944
Aldo Leopold recommends restoring wolves

1960
Program to reduce elk through hunting, shooting, relocating

1968
End of elk reduction program; about 3172 elk in NR

1972
Cougar spotted in park

1976
Winter "meat locker hunt" begins

Late 1980s
Lake trout introduced to Yellowstone Lake; cutthroat (shown) decline

Late 1988
Moose populations are slow to recover from major fire

1994
Elk population 19,000 in NR

1995
Wolves reintroduced

2010
NR elk population 4635
Meat locker hunt ends

2013
95 wolves in park, 34 in NR

2014
4900 bison in park
3.6 million human visitors

genetic analysis and documenting kill sites. They have also set up camera and video traps at dens, trails, and kills, enabling them to witness behaviors rarely seen before. "Everyone talks about cougars being solitary animals," Stahler said. "But the videos are revealing that they're more social than we'd realized," for instance leaving scent markings to communicate with one another.

Preliminary data show that at least 22 cougars have colonized the northern range, the same area that wolves and elk prefer. Stahler suspects that the cats' population may be close to that of the wolves' in this area, about 35—and they may kill more elk than wolves do. Each adult cougar in the northern range killed about 52 elk each year, studies have shown. A wolf takes about 22 elk per year. The cats kill more because they stash their prey and then typically lose much of the carcass to other predators, often a wolf.

Around 2013, cougars turned to eating more mule deer than elk. "We weren't tracking them, so we can't say when or why they made this switch, or if it will last," Stahler said. "The lower numbers of elk may have made room for more mule deer." That kind of change, a sign of growing biodiversity, is exactly what ecologists had predicted that carnivores—whether feline or canine—would bring to Yellowstone.

Although good for the park, such diversity adds extra complexity to all of those natural experiments. Many biologists say that another, often underestimated predator also affects elk and therefore the rest of the ecosystem: the grizzly bear. Some 150 inhabit the park, and they target newborn elk. Although the bears' numbers haven't grown appreciably since the wolves came back, their appetite for tiny elk has ballooned, thanks to another case of human meddling—this one involving fish.

In the late 1980s and early 1990s, nonnative lake trout were moved into Yellowstone Lake, explains Todd Koel, a conservation biologist at the park who specializes in fisheries. No one knows who did the deed, but the results proved catastrophic for the native cutthroat trout, whose numbers plummeted. That in turn hurt the grizzlies, which once gorged on spawning cutthroat in streams every spring, as scientists explained in a 2013 study in the *Journal of Wildlife Management*. "The fish were one of the bears' major sources of energy after hibernating," says David Mattson, an ecologist and grizzly bear expert at Yale University.

But lake trout don't spawn in streams, and they live at depths beyond the reach of the bears. Without cutthroat trout, the bears turned increasingly to another meaty

item that showed up each spring: newborn elk. "Every elk population within grizzly bear areas has declined," Mattson said. This web of trout-bear-elk offers another, often forgotten lesson, these ecologists say: Terrestrial and aquatic ecosystems aren't separate spheres, but are tightly linked.

WHATEVER DROVE THE ELK'S DECLINE, it has turned out to be good news for many other species, including bison, which compete with elk for food and habitat. Today, bison number more than 3500 on the northern range, up from about 250 in 1966 (and only 21 in 1902). "Elk were the drivers of Yellowstone's ecosystem for the last 100 years," Smith says, "but now their star is dimming. Bison are on the rise"—setting the stage for yet another natural experiment.

This one, however, is complicated because bison are heavily managed. Those that wander too far beyond park boundaries are rounded up like livestock, corralled, and culled, because they carry brucellosis, a disease easily transmitted to cattle. With so many bison confined to the northern range, the 1-ton-truck-sized animals are cropping woody plants that had been recovering from the elk, says Ripple, who reported on this with OSU's Robert Beschta last year in *Ecohydrology*. So far, the bison have proven to be too dangerous a prey for wolves to make any dent in the numbers of this big ungulate.

Beavers, too, are prospering. Once common in the northern range (25 colonies were counted in the 1920s), they almost vanished in the 1950s after the abundant elk consumed the willows and aspen, which beavers need for food and building dams. After the wolves came back, Ripple and Beschta documented the regrowth of woody plants along several northern range drainages. A year after the wolf restoration, there was one beaver colony in this area; now there are 12.

But beaver habitat has not recovered as fast as researchers expected. In some areas, the willows remain stunted even when not heavily browsed. "They are not restored," says CSU's Hobbs. To find out why, he and CSU ecologist David Cooper are conducting the only controlled, gold-standard experiment in Yellowstone. The park generally does not allow the ecosystem to be physically altered, but it made an exception after the National Research Council urged a study of beavers and willows.

In 2001, Hobbs and Cooper built dams on four streams to imitate those of beavers, creating pools. They fenced both dammed and undammed areas to exclude browsing animals, mimicking the effects of wolves. After a decade, as they reported with Kristin Marshall in the *Journal of Ecology* last year, only willows in plots that were both dammed and fenced were fully restored.

Willows need more than wolves, the team concluded. They need beavers to raise the groundwater table, so their roots have a steady supply of water, and to create the mud flats where their seeds can sprout. The Catch-22 is that the beavers can't return until the willows do. Although the rodents have recolonized larger rivers, such as the Lamar, they've been slow to return to many smaller streams. Hobbs thinks that's because while the wolves were gone, the elk induced a change of state, turning some riparian areas into grasslands inhospitable to willows.

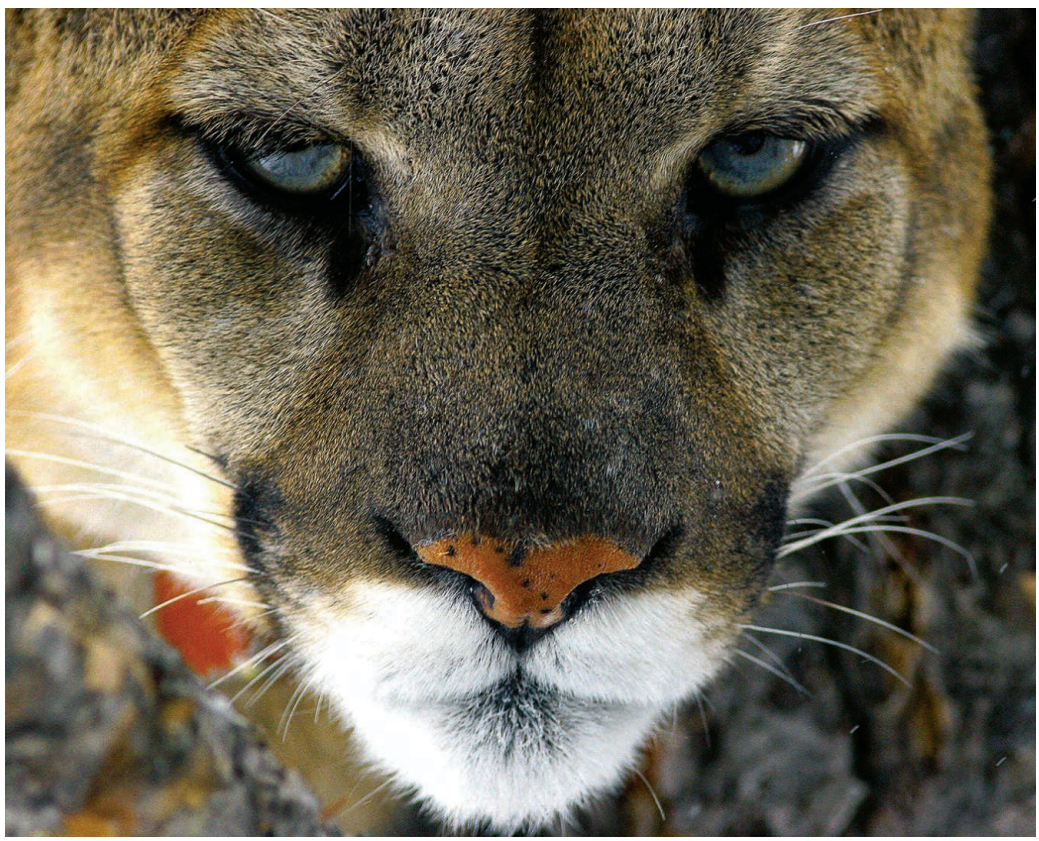
It's not clear when—or if—that will change. Although beavers have been spotted along some of the willow-stunted streams, they have yet to build durable dams. "It may be that the elk population is only now reaching a level that's low enough for a reversal of the effects of over-browsing," Hobbs says. "That's why our experiment is continuing."

These new data have scientists backing away from the idea that the reintroduction of the wolves has fully restored Yellowstone's ecosystem. Instead, they believe that the park—or some parts of it—remains in a state of recovery, struggling with the legacy of the predator removal decades ago.

To Hobbs, one key lesson is just how long a landscape can be scarred. "Those profound effects are difficult to reverse. In some parts of Yellowstone, it's doubtful you'll ever get back to the original state, which is why maintaining an intact ecosystem is so important."

Other scientists, such as Ripple and Beschta, are more hopeful. "It's only been 2 decades" since the wolf reintroduction, Ripple says, "and look at all that's happened and all we've learned."

Manning agrees. "People will look back in 200 years and see the return of the wolves [to Yellowstone] as a profound moment in restoration ecology," he says. "Yellowstone set a benchmark for the rest of the world." And in conservation and restoration biology, fields that are all too often burdened with setbacks and losses, those inspirational effects may be the most important of all. ■



Once exterminated, cougars are back in Yellowstone, although heavily hunted outside the park.

PHOTO: DANIEL STAHLER/NPS