

# Born to Roam: Tracking the Drama of Earth's Ungulate Migrations

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*Wildebeest migration in Serengeti National Park, Tanzania. Each year, enormous herds of wildebeests and zebras move across the Serengeti and into the Masai Mara. The herds have a pivotal role in maintaining the ecosystem.*

*Photograph: Daniel Rosengren CC BY 4.0, via Wikimedia Commons.*

Not all those who wander are lost.

—J. R. R. Tolkien, *The Fellowship  
of the Ring*

**R**ed dawn streaks across the savanna in Tanzania's Serengeti National Park. Somewhere in the distance, hooves drum a staccato beat.

Within minutes, swishing tails and swirling dust cast a shadow over the horizon as hundreds to thousands of wildebeests thunder north toward

Kenya's Masai Mara and greening grasses. Everything about the animals says, "We were born to roam."

In the wake of monsoonal rains that nourish the Masai Mara plains, some 1.3 million wildebeests (and 200,000 zebras) pound across the Serengeti to the Masai Mara. It's a cliffhanger replete with attackers like crocodiles waiting in the shallows of the Mara River. The river runs from Kenya to Tanzania, cutting across the wildebeests' migration route.

This confusion of wildebeests, as it's known for the noise and helter-skelter wanderings of the ungulates, turns into all-out chaos as they sprint through the Mara's treacherous waters. Wildebeests that make it across reach a promised land: lush grazing pastures.

The age-old river crossing scene replays every year from August through October, timed with seasonal rains. It may be the last thriving wildebeest migration in East Africa, report Joseph Ogutu, of the University of Hohenheim in Stuttgart, Germany, and his colleagues in a 2019 paper posted on *bioRxiv*.

### Ungulate migrations under siege

Around the world, according to Ogutu and colleagues, migratory ungulates such as the wildebeest—which rely on movement to find food, water, and calving grounds—are under threat. "Their migrations are being cut off by fences, settlements, farms, roads, and other developments, and the areas where they roam are getting smaller," writes Ogutu's team. "The animals also face the challenges of poaching and having less food to eat because of livestock overgrazing and agriculture."

As *National Geographic* succinctly stated in a November 2010 article on great migrations, "Beasts take off. Humans interfere." The Great Plains of North America are a classic example of human interference in animal migration. According to the United Nations Environment Programme, American bison once numbered as many as 30 million. Today, only a few remnant populations survive, primarily due to past overhunting. In Central Asia,



***Saiga antelope, which inhabit the steppes of Eurasia, underwent precipitous declines as climate change created ideal conditions for disease. Now there is cautious optimism as populations have rebounded.***

***Photograph: Andrey Giljov, CC BY-SA 4.0.***

saiga antelope plummeted from more than a million individuals in 1980 to 334,000 in 2019, a precipitous decline attributed to climate change creating ideal conditions for disease.

Thanks to recent conservation efforts, the saiga antelope is now rebounding from the brink of extinction. Today, some 1.32 million of these animals roam the steppe grasslands of Kazakhstan, according to the Association for the Conservation of Biodiversity of Kazakhstan and other organizations that cosponsor the Altyn Dala Conservation Initiative. The project is an effort to bring back the saiga by using satellite tracking to understand their movements and by increasing anti-poaching activities. Scientists are working to establish more than 4 million hectares of protected areas to benefit the saiga and other steppe wildlife species. Researchers hope for the same outcome for other threatened migratory ungulates.

To better understand the relationship between ungulate movement and human interference, Ogutu's group analyzed trends in East Africa's five migratory wildebeest populations. The scientists used maps, literature reviews, present-day aerial surveys, and data from GPS-collared animals to assess how wildebeest migration routes and populations have changed over time. The researchers found extreme declines in the numbers of migrating wildebeests, and losses of most migration routes in Kenya and Tanzania. "Four of the five current migrations are severely threatened and have virtually collapsed," they state.

The Greater Amboseli, Mara-Loita and Athi-Kaputiei wildebeest migrations have crashed by 85%, 81%, and 95%, respectively, since 1977, whereas the Tarangire-Manyara migration has declined some 72% since 1990. Only the Serengeti-Mara wildebeest migration has remained stable, at some

1.3 million animals, Ogotu's team reported.

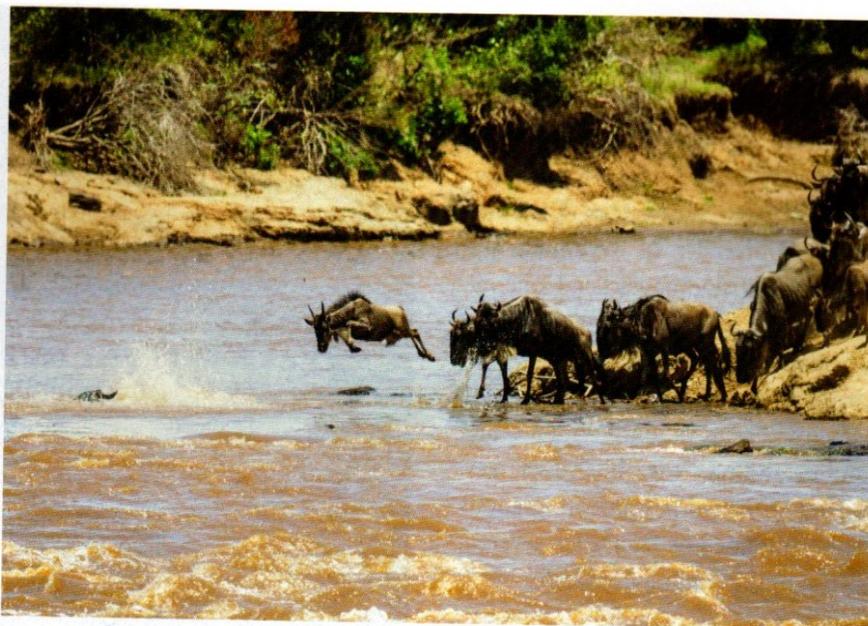
“Wildebeest migrations are mostly in trouble, except for the Serengeti,” says ecologist Craig Packer of the University of Minnesota, who has studied predator-prey dynamics in Africa for more than 30 years. “The Serengeti is the only place where protected areas were specifically designed to enclose the migration. Everywhere else, only dry season refuges were protected.” In those cases, Packer says, “the migrants traditionally left their dry season refuges during the rains, but habitat degradation outside the protected areas cut off migration routes and destroyed wet season pastures.”

Grant Hopcraft of the University of Glasgow, who has conducted extensive research on wildebeest, agrees. “The Serengeti is probably one of the best-protected ecosystems in terms of wildebeest conservation. Where else can you see one million wildebeest migrating?”

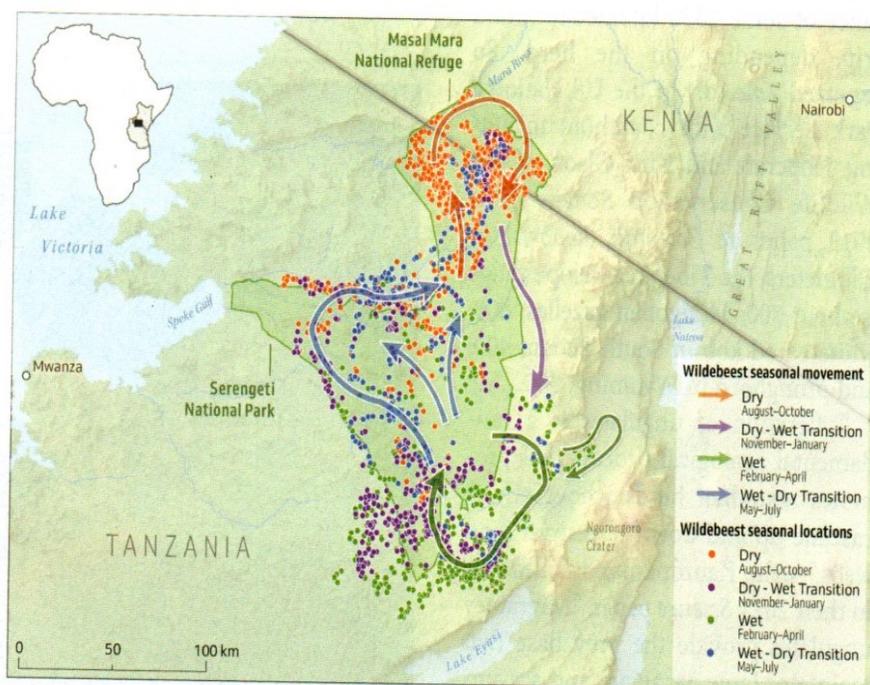
With two wet seasons per year, the Serengeti-Masai Mara ecosystem is an endless cycle of drought and downpour—and hooves in search of greening grass. They're “green wave surfing,” according to Hopcraft, something many ungulates do to find and follow the earliest available and most nutritious plant growth as it sprouts up across the landscape in spring.

In the Serengeti-Mara, the “short rains” arrive in November and December, driving the migrants south. Heavy “long rains” fall in March, April, and May. As the rains abate, the greening of the plains jump-starts ungulates' return journeys north and west. The huge herds till the grassland with their hooves, influencing the entire savanna ecosystem.

Saving these and other migrations, say Ogotu and coauthors, means securing more land, partnering with local communities, and reducing our human footprint. “In particular,” Ogotu and colleagues write, “regulation of livestock numbers, fences, settlements and roads” is needed. The intense droughts that have become more frequent make these changes



*As part of the Great Migration, as it's termed, wildebeests line up to cross the Mara River in Kenya's Masai Mara National Reserve. Photograph: Danijel Mihajlovic, CC BY-SA 4.0.*



*In cycles of monsoonal rains that nourish the Masai Mara plains, some 1.3 million wildebeest and 200,000 zebras cross the Serengeti and into the Masai Mara on a loop migration each year. It's one of the largest remaining terrestrial animal migrations in the world. Image: Movement data from Grant Hopcraft, University of Glasgow; cartography by Ian Freeman.*

more urgent, according to Ogotu. Drought makes it more difficult for ungulates to follow the wave of progressively greening vegetation.

“The consequences of not acting will be huge,” Ogotu says. “Migrations of zebras and Thomson's gazelles in

Kenya's Rift Valley have already been lost. Wildebeest could go the same way.” Like any migratory species, Hopcraft adds, “if the entire route cannot be secured, the population is destined for collapse regardless of how abundant the animals are.” But do scientists know

where these routes run? Researchers now realize that, in many cases, what's missing is a migration map.

Mitigating adverse impacts on ungulates is “thwarted by a singular challenge,” stated Matt Kauffman of the University of Wyoming and coauthors, including Packer, Hopcraft, and others, in 2021 in *Science*. “Most ungulate migrations have never been mapped in sufficient detail to guide effective conservation.” Without that understanding, the biologists say, “many of the world’s great migrations will continue to be truncated, severed, or lost in the coming decades.”

### Going, going...gone

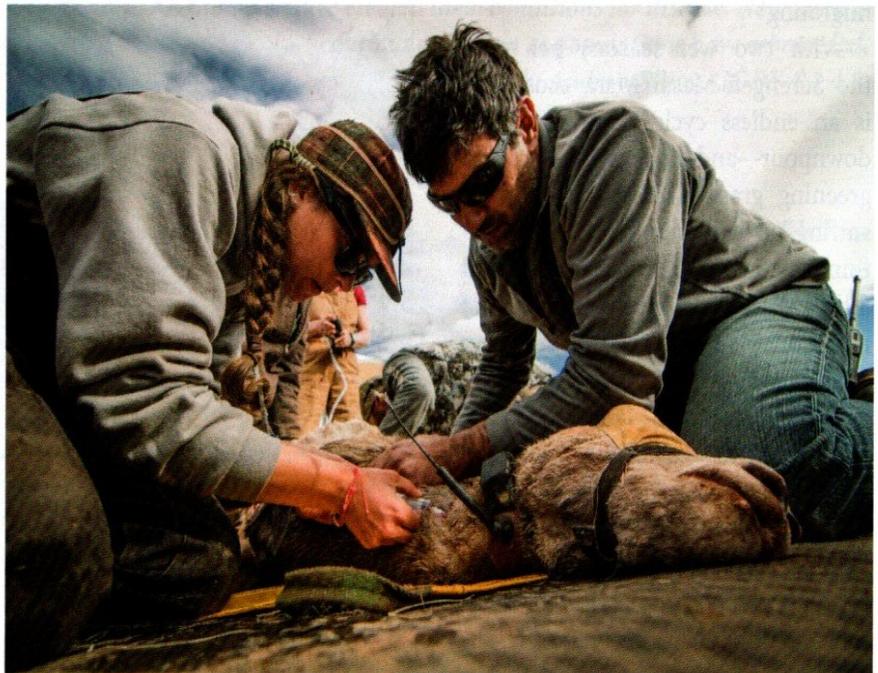
Ungulates hoof it across landscapes on every continent but Australia and Antarctica. Caribou or reindeer (*Rangifer tarandus*) are the longest ungulate migrators, covering a distance of some 1350 kilometers round trip, depending on the herd. So reported Kyle Joly of the US National Park Service with coauthors including Hopcraft and Kirk Olson of the Wildlife Conservation Society in a 2019 paper in *Scientific Reports*. In kilometers, the Tibetan antelope range is about 700; Mongolian gazelles, 600; white-eared kob in South Sudan, 400; and pronghorn in Wyoming, 300.

“Migration of ungulates is a fundamental ecological process that promotes abundant herds whose effects cascade up and down terrestrial food webs,” write Kauffman and colleagues in their 2021 *Science* paper. “Migratory ungulates provide the prey base that maintains large carnivore and scavenger populations and underpins terrestrial biodiversity.” But, these authors state, “ungulate migrations are disappearing at an alarming rate.”

Millions of Cape springbok that once traversed the Karoo landscape of South Africa are gone, lost to fences, disease, and hunting. On Russia’s Kola Peninsula, a railroad divided the reindeer population and effectively ended the longest of the region’s migrations. One railroad may be the least of it, however. According to Kauffman, some 25 million kilometers of new



*Mule deer in southwest Wyoming move from higher areas in the Wyoming Range where they spend the summer to wintering areas at lower elevations. Photograph: Tom Koerner/USFWS Mountain-Prairie, via Wikimedia Commons.*



*Biologist Matt Kauffman and colleagues collar mule deer that undertake a 241-kilometer-long migration across Wyoming. The scientists are working to understand the benefits of long-distance migrations and threats to their persistence. Photograph: Ben Kraushaar.*

roads may be built worldwide by 2050, further severing seasonal migrations.

The effects of climate change are also looming. They may result in a trophic mismatch if individuals cannot adjust the timing of their migrations

to follow earlier spring green-up, states Katherine Malpeli in the 2022 US Geological Survey (USGS) report *Ungulate Migration in a Changing Climate*. “Does earlier spring green-up make ungulates leave their winter

ranges sooner?” she asks. “Do persistent drought conditions reduce the carrying capacity of seasonal range habitats or lead to shifts in migration pathways? These and other questions remain largely unanswered.”

A hint comes from research by Ellen Aikens and others at the University of Wyoming. The scientists reported in *Global Change Biology* in 2020 that drought limits the spring green-up duration and dramatically shortens the annual foraging bonanza of mule deer.

### It takes a map

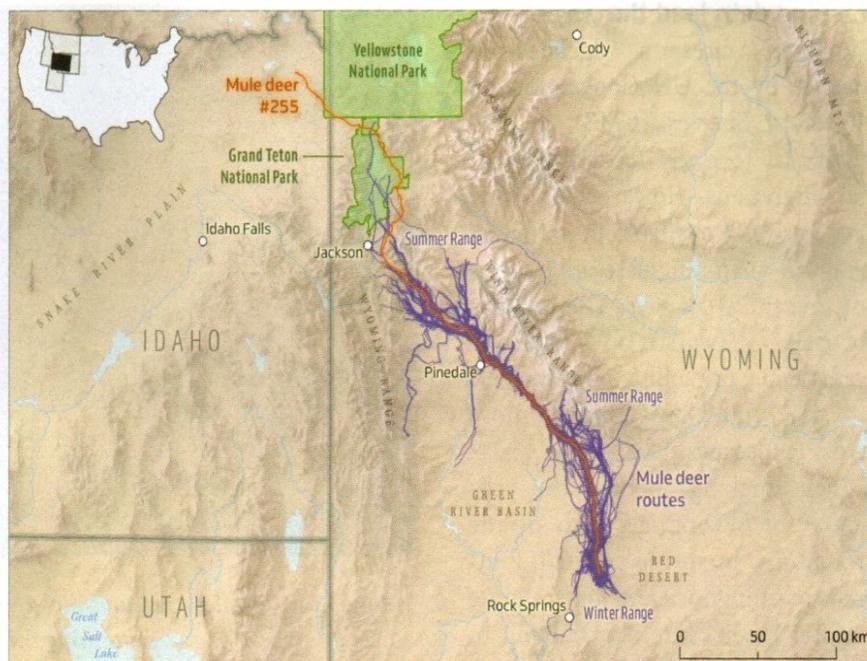
Kauffman believes that “detailed mapping, currently lacking, is needed to guide the conservation solutions necessary to maintain migrations over the long term.”

Enter animal tracking data sets, historical records, and local and Indigenous knowledge. “They can form the basis for a global atlas of migrations designed to support conservation action and policy at local, national and international levels,” Kauffman and coauthors write in *Science*. “New technologies have enabled precise mapping of long-distance migrations and are revealing that the movements of ungulates across the globe are more diverse and behaviorally complex than previously recognized.”

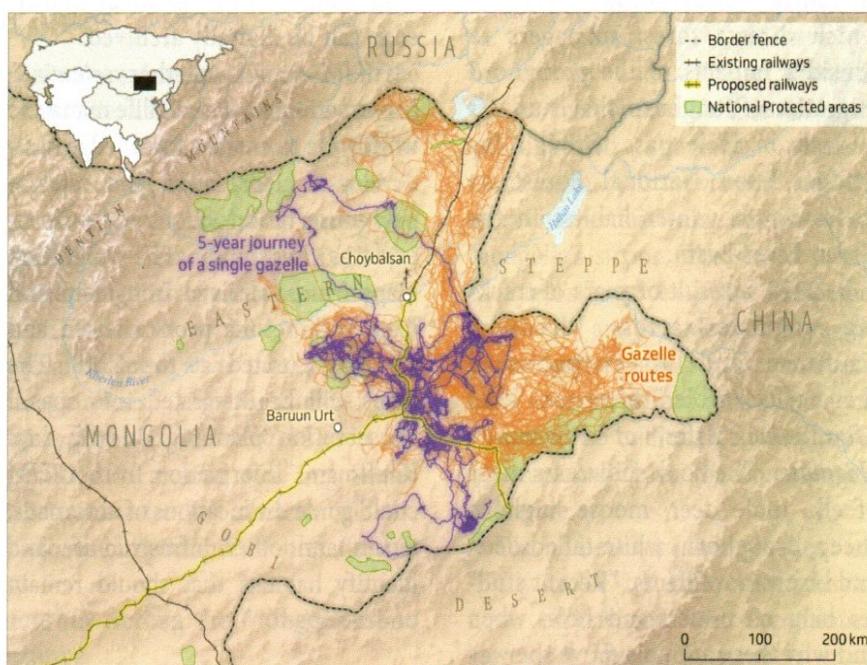
When animal tracks are overlaid on maps of seasonal resources, they show everything from long-distance movements across climate gradients to shorter elevational movements to reach cooler alpine habitats. “Detailed movement data are leading to new ecological discoveries,” the scientists report.

For example, on the Mongolian steppe, gazelles explore an area about the size of Hungary, or 100,000 square kilometers, over their lifetimes. In Ethiopia’s Gambella National Park, the white-eared kob migration connects to the species’ Boma–Bandingilo migration in South Sudan, extending the animals’ known travel route.

In some ungulates, migration reflects culture learned and transmitted from generation to generation. “In North America,” Kauffman’s



**A map of Wyoming’s Red Desert-to-Hoback mule deer migration is providing a way of identifying opportunities to keep this corridor open. Mule deer no. 255 extended the species’ record-holding migration. Image: Data from Matt Kauffman and the US Geological Survey; cartography by Ian Freeman.**



**Usually nomadic in their movements, Mongolian gazelles are the most numerous wild ungulates on Mongolia’s steppe. One such gazelle trekked 18,000 kilometers across the steppe. Image: Movement data from Thomas Mueller, Senckenberg Biodiversity and Climate Research Centre; cartography by Ian Freeman.**

team relates, some “bighorn sheep and moose failed to migrate when first translocated into new landscapes. Over multiple generations, however, populations gained the knowledge to move seasonally and

find forage at broader scales and became more migratory.” The persistence of migration may depend on the survival of individuals who know the route and can pass it on to the next generation.

### Tracking data lead the way

Kauffman cites a decades-old advance by the UN Convention on Migratory Species (CMS), a 1979 move that formally recognized animal migrations. However, “tracking data were not available in sufficient detail to map ungulate migrations until recently,” he says. The increasing use of GPS collars on wildlife, for example, is providing new insights into where and how animals move across landscapes.

Such tracking sparked the protection of Wyoming's Path of the Pronghorn. In spring and fall, hundreds of pronghorn antelope migrate between their summer habitat in Grand Teton National Park and their winter range in the Green River Valley of southwestern Wyoming. A map of pronghorn routes is included in the Bridger-Teton National Forest Plan, first completed in 1990 and currently undergoing revision, which directs forest managers to consider impacts to the pronghorn migration. Pronghorn that summer in Jackson Hole pass through the Bridger-Teton National Forest on their way to winter habitat in the Green River Basin.

In 2018, a result of years of tracking ungulates across Wyoming, Kauffman and others published the coffee table reference *Wild Migrations: Atlas of Wyoming's Ungulates*. The book showcases maps of elk, mule deer, moose, bighorn sheep, pronghorn, white-tailed deer, and bison movements. “Recent studies help us understand how, when and why these animals move the way they do,” the scientists write in the atlas. “Such findings are informing new approaches that are key to sustaining these migrations.”

The Wyoming atlas and other projects ultimately spawned a new effort called the Global Initiative on Ungulate Migration (GIUM) under the auspices of the CMS. “Developing a global atlas of ungulate migrations will require unprecedented collaboration to assemble the required knowledge, data and



*Mongolian gazelles are nomadic ungulates whose movements play a key role in sustaining the most intact steppe ecosystem in the world.*

*Photograph: Thomas Mueller.*

analytical tools,” state Kauffman and colleagues in *Science*. “Unmapped migrations can be targeted for new field studies, and historical knowledge can be digitally archived.”

GIUM brings together scientists, conservationists and wildlife managers worldwide to create a knowledge base, develop a global atlas, and catalyze new conservation actions and policies, explains Kauffman. The migration maps will be derived from empirical data, with results peer-reviewed and centrally curated at the CMS. The maps will be integrated into spatial conservation planning. Ideally, says Kauffman, “information from GIUM could guide the locations of new roads, fences and other infrastructure and identify habitats that should remain undeveloped.”

### Mapping iconic migrations

In the US West, such mapping is already underway. After the release of *Wild Migrations*, a series of detailed maps followed. Published by the United States Geological Survey, *Ungulate Migrations of the Western United States*, volumes 1 (2020) and 2 (2022), reveal migration pathways in more detail.

“Many ungulates have to migrate to thrive on the strongly seasonal landscapes of the American West,” says

Kauffman, the report's lead author. “These maps make it possible to manage those critical movements.”

Each spring and fall, ungulates move in sync with their food resources. But they increasingly face obstacles such as new subdivisions, high-traffic roads, and climate change effects such as drought. Detailed mapping from GPS collar data, like that provided in the *Western Migrations* series, “tells us where the animals need to go and helps us pinpoint barriers,” says Kauffman. “Having free movement along corridors allows ungulates to adapt to climate change by migrating early or late, or moving faster or slower.”

Researchers have long tracked animal movements as a cornerstone of state monitoring and management efforts, but extracting the most meaningful population-level migration corridors from a tangle of individual animal tracks has been technically complex, they say. Seeking answers, a corridor mapping team was established in 2018 with participation from biologists at state wildlife agencies, tribes and the USGS. The team created Migration Mapper, new software to develop the maps published in volumes 1 and 2 of *Ungulate Migrations of the Western United States*.

### Deer with a mind of her own

Among the migrations tracked are those of Wyoming's Sublette mule deer herd. Twice a year, these deer migrate between their winter range in the Red Desert sagebrush and their high-elevation summer range 240 kilometers north, in the Hoback Basin. The trip allows the deer access to nutritious forage as sagebrush and grasses green up throughout the spring.

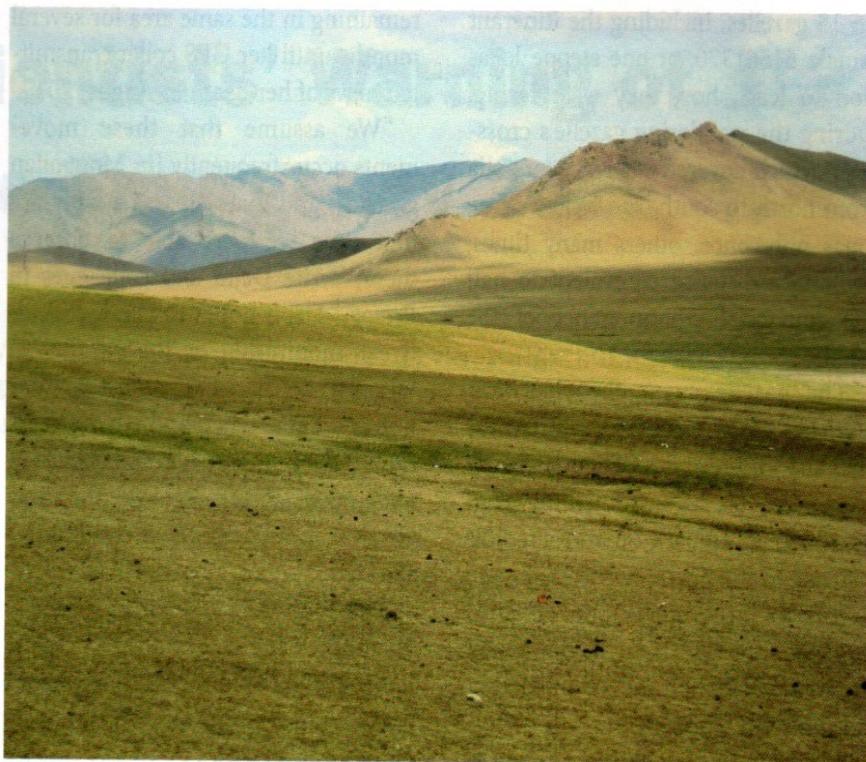
The route also places numerous obstacles in their path, from housing developments to shopping centers. In 2001, the Sublette herd was estimated at 34,700; by 2017, it had declined by some 50% to 17,299. According to Wyoming Game and Fish Department biologists, downturns in the Sublette mule deer herd since the early 2000s can likely be attributed to loss of winter habitat and mortality in severe winters.

Despite the challenges, mule deer show high fidelity to their migration routes and seasonal ranges—usually. A doe known as deer number 255 (she's the 255th mule deer GPS-collared in one of Kauffman's studies) has led the biologists on a merry interstate chase.

In 2016, 255 made a world-record migration from the Red Desert over the Teton Range. Deer 255 wintered near Superior, Wyoming, then migrated to the Hoback Basin. By itself, this 240-kilometer journey is the longest-distance deer migration in America. But unlike other mule deer that settled in at the Hoback Basin for the summer, 255 kept going, circling the western edge of the Gros Ventre Range toward Jackson Hole.

Deer 255 trekked across the head of Cache Creek near the town of Jackson. Then she crested the pass between Nowlin Peak and Jackson Peak, the highest point on her route. Undaunted, 255 kept going, navigating busy highways, barbed-wire fences, and other hazards. She ultimately entered the Henry's Fork caldera, finally reaching her summer range and ending that season's migration.

It was 15 June, and the doe was in the woods on the outskirts of Island Park, Idaho. This patch of meadows,



*The Mongolian steppe ecosystem: This grassland is known for its distinctive wildlife, in particular, its vast movements of Mongolian gazelles.*

*Photograph: Francisco Anzola. CC BY 2.0.*

wetlands and lodgepole pines was the habitat she had been migrating toward since 20 March. She was 389 kilometers from where she'd started in southwest Wyoming. That made hers the longest-distance spring migration documented to date in a mule deer.

"This deer shows the connectivity of the landscape in a way that exceeds our imaginations," says Kauffman. "The mule deer herd in the Red Desert has persisted in making epic migrations, a testament to their tenacity and the biological importance of migration."

### Journey across the Mongolian steppe

Deer 255 has a tiny migratory range compared to that of her distant cousins in Mongolia. There, over 5 years, one Mongolian gazelle whose GPS collar ID was 61561370 trekked 18,000 kilometers across the steppe. "Her journey was extraordinary, not only due to its sheer length but because she frequently ventured for hundreds of kilometers into regions she had not used previously," write Kirk Olson, Nandintsetseg Dejid, and Thomas Mueller of Germany's Senckenberg

Biodiversity and Climate Research Centre, in February 2022, in *Ecology*.

Mongolian gazelles, usually nomadic in their movements, are the most numerous wild ungulates on Mongolia's steppe. The steppe is one of Earth's most extensive temperate grasslands, and the Mongolian gazelle is among the planet's most numerous large animals, with a total population of around 1.5 million, according to the International Union for Conservation of Nature.

Olson believes the gazelles are "likely to be tested in ways they've never experienced, with a continued increase in livestock numbers eroding their habitat, and construction of railroads bisecting their range. Degradation from chronic overgrazing and barriers to movement are serious threats." Conservation interventions, he says, "range from creating gaps in existing infrastructure for crossing options, preventing additional barriers from being constructed, and reducing [grazing] livestock numbers without harming livelihoods."

In October 2014, Dejid, Olson and other researchers placed GPS collars

on 15 gazelles, including the itinerant female 61561370, at one steppe location to learn how they were faring. During the wandering gazelle's crossings, which covered eastern Mongolia from north to south, she visited some areas only once, others many times, walking a distance equivalent to half the equatorial circumference of the Earth.

The gazelle spent the first year after her collar placement near where she had received it. "Then, in early November of 2015, something triggered her to embark on an incredible journey to the north," write Dejid and coauthors in *Ecology*. She revisited the place she had been in the winter of 2014–2015, then moved northeastward toward China.

After running up against an impenetrable border fence, she headed north across two major rivers, the Kherlen and the Ulz, waterways then frozen. In January 2016, she reached northern Mongolia, near the border with Russia. In addition to border fences, the gazelle skirted oil fields, villages, and mining operations. After thousands of kilometers of explorations, in January 2019, she returned to an overwintering area she had used 2 years earlier. There, she ceased her travels,

remaining in the same area for several months until her GPS collar transmitted news of her death in August 2019.

"We assume that these movements occur frequently [in Mongolian gazelles] and that this was simply the first time we were able to observe them," write Dejid and colleagues in *Ecology*. Dejid hopes to conduct multiyear monitoring of the gazelles to "allow researchers to demonstrate how nomads know when and where to go, how they find suitable conditions in wide-open, intact regions, and how far away they detect those conditions," she states.

The multiyear trek of one gazelle "highlights the importance of maintaining highly permeable landscapes for nomadic ungulates," Dejid concludes, "allowing them to locate dynamic resources and to escape local, extreme events" such as severe weather. For example, in September 2007, precipitation patterns led to unusual conditions in Mongolia's eastern steppe. Severe drought had seared many areas, but heavy rains had fallen 2 weeks earlier in one spot, greening an oasis. More than 200,000 Mongolian gazelles found the site, gathering in a megaherd to graze on sprouting grasses.

Nomadism notwithstanding, clearly not all those who wander are lost. Conservation is a dynamic challenge to protect those who were born to roam. Monitoring methods like tracking have enabled much-needed range mapping, but there is still much to learn about the millions of beasts on the move.

"Primary research needs are the acquisition and analysis of data on ungulate movements to refine delineation of winter range, summer range, and [migration] corridors to support a better understanding of how ungulates use these habitats," writes Malpeli in her USGS report.

The answers have much to tell us about other species, as well. "Migrations are the culmination of millions of years of social, cognitive, physiological, and ecological evolution," says Grant Hopcraft. "They tie ecosystems together. Their loss indicates a larger problem—a loss of ecosystem resilience—around the world."

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*Ecologist and science writer Cheryl Lyn Dybas (Cheryl.lyndybas@gmail.com), who often covers conservation biology for BioScience, admires the spirited deer 255 and gazelle explorer 61561370. Despite incredible challenges, they forged new passages across landscapes.*