Received: 14 April 2021 | Revised: 6 October 2021 | Accepted: 15 October 2021

DOI: 10.1002/ecy.3660

THE SCIENTIFIC NATURALIST

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

A gazelle's extraordinary, 18,000-km-long journey through the steppes of Mongolia

Nandintsetseg Dejid[1] | **Kirk Olson**[2] | **Theresa S. M. Stratmann**[1,3] | **Thomas Mueller**[1,3]

[1]Senckenberg Biodiversity and Climate Research Centre, Frankfurt am Main, Germany

[2]Wildlife Conservation Society, Ulaanbaatar, Mongolia

[3]Department of Biological Sciences, Goethe University Frankfurt, Frankfurt am Main, Germany

Correspondence
Nandintsetseg Dejid
Email: dnandintsetseg@gmail.com

Funding information
German Federal Ministry of Education and Research, BMBF, Grant/Award Number: 01LC1820A

Handling Editor: John J. Pastor

KEYWORDS: animal movement, arid climate, barrier, fence, memory, migration, navigation, nomadism, search, ungulate

Animals in unpredictable environments show a range of adaptations to survive and reproduce, including nomadic movements. Like migratory animals, nomadic animals move long distances, but nomadism differs from migration by the absence of spatially predictable paths from and back to a place of origin (Jonzén & Knudsen, 2011; Teitelbaum & Mueller, 2019). Despite the increasing use of GPS trackers, movement data from individuals are often limited to one or very few years of data, an artifact of battery constraints. Here we report on the extraordinary 5-year journey of a single Mongolian gazelle, *Procapra gutturosa*. Mongolian gazelles are the most numerous wild ungulate on Mongolia's steppe. The steppe is one of the largest temperate grasslands in the world, characterized by a cold, extreme continental climate with unpredictable resources in both space and time (Carbutt et al., 2017).

In October 2014, we deployed GPS collars on 15 gazelles at a single location in the steppe. We have previously analyzed the movement data of these individuals and have highlighted the nomadic and unpredictable nature of their movements (Nandintsetseg, Bracis, Olson, et al., 2019). However, the collar of one of the female gazelles kept functioning long past our initial analyses of up to 3 years. This female gazelle was equipped with a solar-assisted GPS collar that provided hourly location data for almost 5 years. Her journey was extraordinary, not only due to its sheer length but because she frequently ventured for hundreds of kilometers into regions that she had not used previously during the study period (hereafter referred to as unfamiliar terrain). During her journey, she would visit many areas only once but other areas multiple times in an irregular and unpredictable manner. For other gazelles tracked previously, we were unable to collect hourly movement data for more than 3 years. Thus, it is difficult to say if other gazelles could have shown the same extreme movements as this gazelle had, but it is certainly possible.

We were unable to determine the exact age of the female gazelle. However, we captured her as an adult (>2 years) and tracked her for almost 5 years (October

2014 to August 2019), which certainly covered a large portion of her life because the oldest known age for female Mongolian gazelles is 9.5 years (Zhaowen et al., 1998).

Her irregular movements are most apparent by comparing areas where she was during winter and calving seasons each year. Straight-line distances between wintering grounds in different years (average locations of 1 January) were up to 440 km apart, while calving grounds (average locations of 15 June) were up to 275 km apart and were never located in the same region (Nandintsetseg, Bracis, Olson, et al., 2019). While straight-line distances are often used to determining the scale of movements for conservation purposes, the cumulative distance traveled may be ecologically more meaningful. The cumulative distance derived from hourly GPS fixes showed that the gazelle completed a journey of more than 18,000 km, which covered eastern Mongolia from north to south (Figure 1), roughly equivalent to one-half of the equatorial circumference of the Earth. The total continuous lifetime movement of this individual would certainly be even longer because we covered

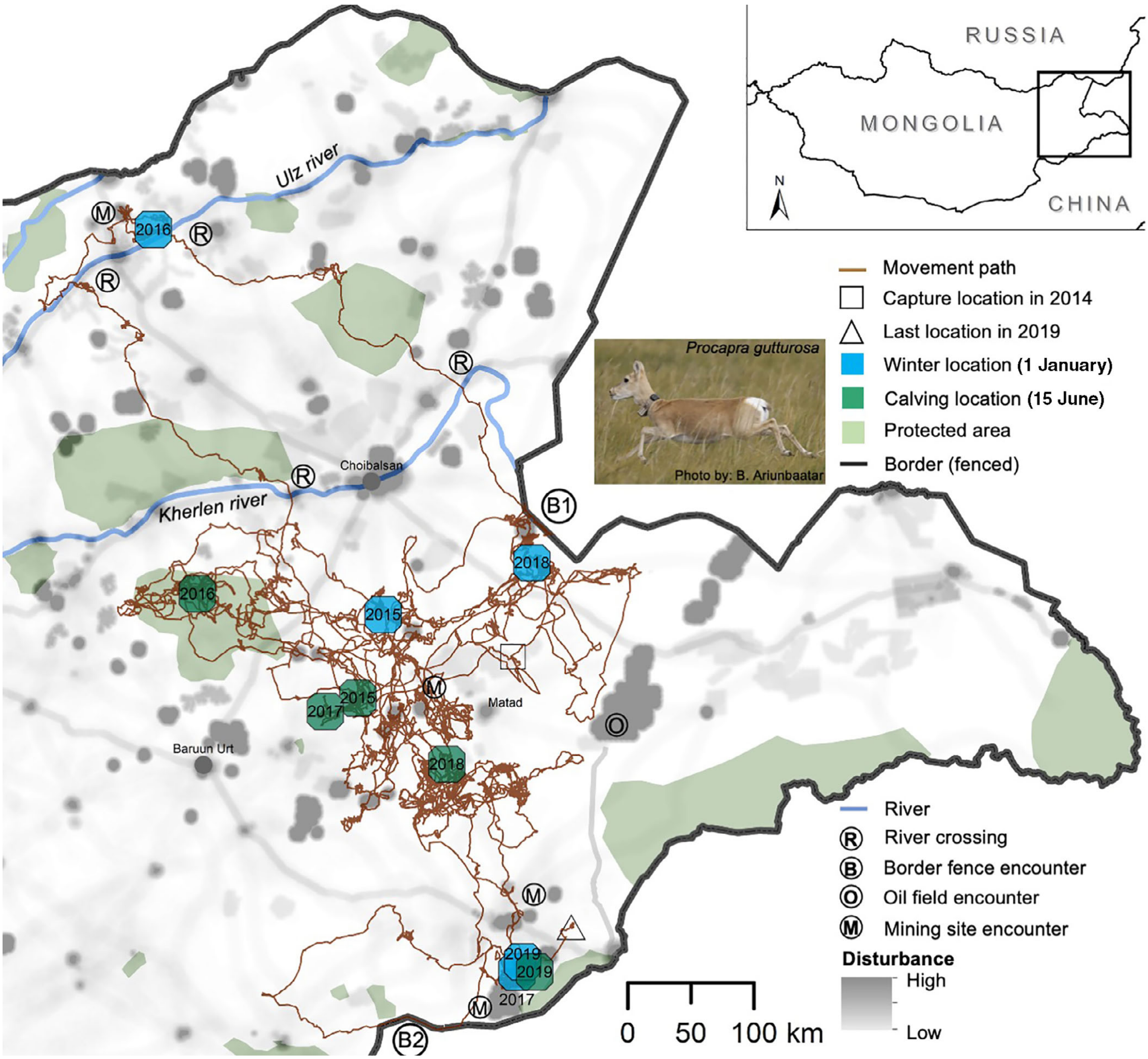

FIGURE 1 The 5-year journey of a female nomadic Mongolian gazelle that traveled over 18,000 km through the steppes of Mongolia. The movement data showed a lack of fidelity to wintering and calving areas. Even though the gazelle used the protected areas at times, she mostly ventured in unprotected areas, encountering permeable and impermeable barriers, including fenced borders, oil fields, and mining sites, as well as areas with human settlements

only a portion of her lifespan and the hourly GPS data omits fine-scale movements.

The first year after we started tracking the gazelle in 2014 was seemingly uneventful, she spent over a year in the vicinity of where she was originally equipped with the GPS collar (capture location, Figure 1). Then, in early November of 2015, something triggered her to embark on an incredible journey towards the north (Figure 1, Video S1 in the Supplementary Material). First, she briefly revisited the area where she had been in the winter of 2014–2015 (winter location 2015, Figure 1) but rather than staying, she first moved northeast towards China. After encountering the impermeable border fence (B1, Figure 1), she traveled northward, crossing two major rivers, the Kherlen and the Ulz, in December of 2015, when the rivers were frozen. In early January of 2016 she eventually reached the hilly terrain of northern Mongolia near the border to Russia (winter location 2016, Figure 1). Monthly snow cover images derived from Copernicus (Muñoz Sabater, 2019) reveal that the region where she started the long-distance journey in November of 2015 was affected by a high snow cover (Figure 2). In the 2 months it took her to reach the snow-free, hilly region near the Russian border (Figure 2), she traveled a cumulative distance of 900 km.

In March of 2016, she moved south, crossing the same rivers. The movement path showed that she was searching for suitable areas to cross Ulz and Kherlen rivers in March and May of 2016, respectively. Crossing these rivers in spring when they were not frozen may have been more challenging than during the height of winter. On her way south, she did not retrace her original route, nor did she stop at the latitude she came from, instead she paused briefly in a protected area during the calving period from mid-June to early July (calving location 2016, Figure 1). She then continued south until she eventually reached another section of the border fence to China in December of 2016 (B2, Figure 1). This journey from north to south covered a cumulative distance of 3400 km (Figure 1). Rather than returning to the

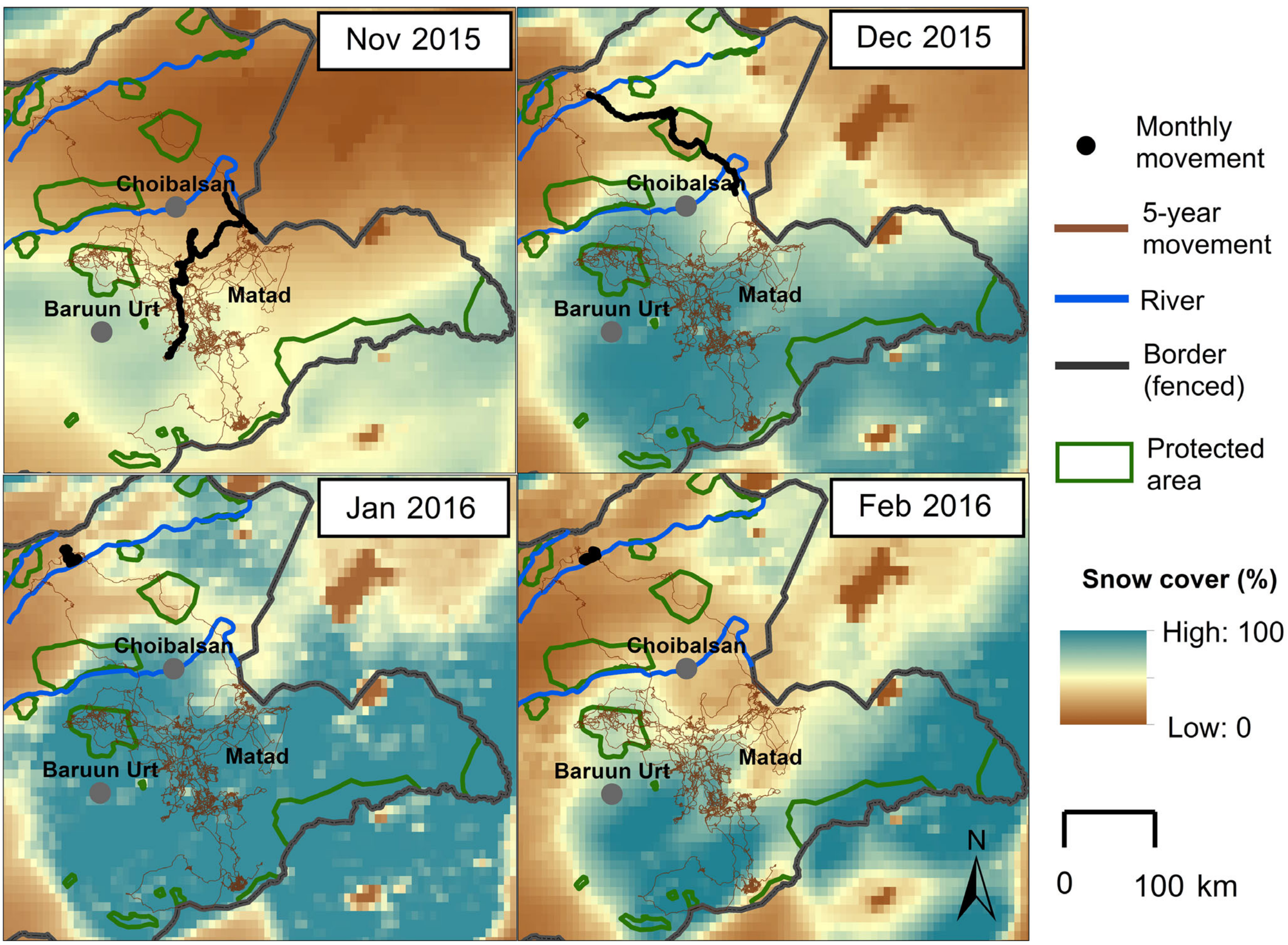

FIGURE 2 Monthly movement paths of a female, nomadic Mongolian gazelle relative to snow cover in the Eastern Steppe of Mongolia. The gazelle avoided areas with high snow cover, moving 900 km in 2 months (upper panels). She eventually overwintered in a hilly region that provided snow-free patches (lower panels)

previous winter refuge in the north (winter location 2016, Figure 1), she overwintered in the far south, again in an area known for its hilly terrain (winter location 2017, Figure 1), 440 km straight-line distance from the wintering ground of the previous year.

As spring arrived in 2017, she first chose to move north. Then, surprisingly, she revisited exactly the same location where we first captured her 3 years ago (capture location, Figure 1) and even at the same time of year (October 2017, Video S1). She encountered the fenced Chinese border, again in the same area she encountered it in November of 2015, and overwintered in its vicinity (B1 and winter location 2018, Figure 1). In the spring of 2018, she moved south and returned to the region she had stayed in during the summer of 2017. She stayed there until the fall of 2018 (calving location 2018), when she again ventured into unfamiliar terrain. This time she moved 90 km along the border fence to China (B2, Figure 1) and completed a more than 400-km-long loop in the southern part of the steppe before finally, in January of 2019, returning to the overwintering area she had used 2 years ago. After that, she was relatively sedentary, remaining in the same area for almost a year until the GPS transmitted her death in August of 2019 (winter and calving locations 2019, Figure 1). The collar was recovered inside a herdsman's yurt who reported that the gazelle appeared to have died from an infestation of maggots on her hip.

While her journey was the most extreme compared to other gazelles we have tracked (Nandintsetseg, Bracis, Olson, et al., 2019), we emphasize that the total number of individuals we have tracked is small (105 individuals) compared to the estimated population size of 1 million gazelles (Mallon, 2008). We therefore assume that the movements described here occur frequently and that this was simply the first time we were able to observe them. Moreover, her journey differed from better-known migratory ungulates including mule deer in Wyoming and wildebeest in the Serengti-Mara ecosystem (Kauffman et al., 2021), due to the lack of regular seasonal movements where individuals return to the same overwintering and calving areas every year.

What was the motivation for her journey and how did she know where to go and when? Some drivers of gazelle habitat selection are known: gazelles seek areas of good forage during the vegetation growing season and avoid areas with deep snow during winters (Stratmann et al., 2021). Less known are whether other factors like high densities of biting flies, predation risk, or other extreme events like fire and droughts may also drive the nomadic movements of gazelles.

Compared to the understanding drivers of nomadic movements, the search and navigation mechanisms for nomadic journeys of ungulates are less known, and likely differ from those of migratory ungulates. What cues did the gazelle use when she made forays into unfamiliar terrains and how did she manage to revisit previously used areas? Is the movement towards unfamiliar terrain due to social interactions and acoustic communication among individuals, or following environmental cues? A combination of search and escape movements from harsh conditions may be at work. For example, the snow storm in the winter of 2015–2016 elicited an extremely long journey that was more directed than other parts of the movement track (Figure 2). In particular, the search for vegetation greenness triggered by unpredictable rainfall in the summer and escape movement from severe weather such as droughts or extreme winters (Dzud in Mongolian) may be key mechanisms of nomadic movements.

In migratory ungulates, where long distance journeys repeat from 1 year to another and follow predictable routes, memory is often a key navigation mechanism (Fagan et al., 2013). Likewise, memory might be important for those nomadic movements that, unlike those of Mongolian gazelles, result from searches for ephemeral but stationary water resources (Nandintsetseg, Bracis, Leimgruber, et al., 2019). Even if our gazelle mostly ventured into unfamiliar terrain, evidence that spatial memory plays a role also exists. For example, she used the same wintering location twice, but 2 years apart. She also returned to the capture location after 3 years and to one protected area three times, indicating that gazelles might have a long-term memory to exploit favorable areas. Gazelles live in fission-fusion groups and observed group sizes ranging from a single individual to more than 200,000 individuals (Olson et al., 2009). In such a scenario, portions of the gazelle's journey likely occurred simultaneously with thousands of others or may have been undertaken individually or in a small group of gazelles. In particular, during the extreme events like droughts and harsh winters, individual knowledge about a location or area may have been less important, instead collective decision making and/or group communication, aided by infrasound vocalization among individuals, may have been key (Couzin et al., 2005).

Recording long-term tracking data simultaneously for a larger number of individuals would be necessary to address questions about navigation mechanisms, group communication, and refuges in the future. While gazelle navigation mechanisms remain largely unresolved, there are important conservation implications of the unpredictable, long-distance movements from this journey (Nandintsetseg, Bracis, Olson, et al., 2019). No movement corridors were identified from the tracking data that could be protected. In addition to border fences that create an artificial range boundary, this gazelle encountered areas of high disturbance, such as oil fields, villages, and mining operations (Figure 1). Protected areas played a limited role in maintaining the movements. The gazelle encountered four formal protected areas, only spending significant time in one of them and briefly passing through the others (Figure 1). Additionally, the locations of the gazelle during the calving and wintering periods were outside of the protected areas, indicating the intactness and integrity of much of the gazelle's range.

The multiyear journey of our gazelle highlights the importance of maintaining highly permeable landscapes for nomadic ungulates, allowing them to locate dynamic resources and to escape local, extreme events. Importantly, long-term data from individuals are essential for discovering behaviors that are not observed in short-term movement data. For example, this gazelle could have been described as a resident individual, and long-distance movements that were likely crucial to the long-term survival of the gazelle would not have been observed if the data had been collected for only a year. Also, longitudinal data informs effective management measures, such as promoting policies that maintain landscape permeability and the scale and heterogeneity of conservation areas. For example, hilly regions that provide snow-free patches are essential to gazelles' survival during at least some winters, which indicates that there should not be impermeable barriers bisecting the northern and southern regions of the Eastern steppe. These challenges are shared among a number of dryland ungulates that are considered nomadic or semi-nomadic and threatened by habitat fragmentation. The characterization of nomadic behavior in ungulates is only beginning to be appreciated and conservation strategies have yet to be fully developed. It is therefore imperative to continue to advance our knowledge of such movements so that suitable conservation measures can be developed.

ACKNOWLEDGMENTS

We are grateful to numerous field assistants and the World Wildlife Fund for Nature Mongolia (WWF Mongolia), which helped with obtaining the capture permit (6/5621). The gazelle was captured following standard protocol approved by the Ministry of Environment and Green Development in Mongolia. This study was funded by the Robert Bosch Foundation and the German Federal Ministry of Education and Research (BMBF, 01LC1820A).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

GPS movement data are sensitive and cannot be posted publicly. Researchers seeking additional detail and the data are encouraged to visit the MoveBank repository and information under Study Name "Mongolian gazelle, Dejid, Eastern Steppe in Mongolia."

ORCID

Nandintsetseg Dejid https://orcid.org/0000-0002-5376-3808
Thomas Mueller https://orcid.org/0000-0001-9305-7716

REFERENCES

Carbutt, C., W. D. Henwood, and L. A. Gilfedder. 2017. "Global Plight of Native Temperate Grasslands: Going, Going, Gone?" *Biodiversity and Conservation* 26(12): 2911–32. https://doi.org/10.1007/s10531-017-1398-5

Couzin, I. D., J. Krause, N. R. Franks, and S. A. Levin. 2005. "Effective Leadership and Decision-Making in Animal Groups on the Move." *Nature* 433(3): 513–6. https://doi.org/10.1038/nature03236

Fagan, W. F., M. A. Lewis, M. Auger-Methe, T. Avgar, S. Benhamou, G. Breed, and T. Mueller. 2013. "Spatial Memory and Animal Movement." *Ecology Letters* 16(10): 1316–29. https://doi.org/10.1111/ele.12165

Jonzén, N., and E. Knudsen. 2011. "Uncertainty and Predictability: The Niches of Migrants and Nomads." In *Animal Migration: A Synthesis*, edited by E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, 91–109. Oxford: Oxford University Press.

Kauffman, M. J., F. Cagnacci, S. Chamaillé-Jammes, M. Hebblewhite, J. G. C. Hopcraft, J. A. Merkle, and S. Zuther. 2021. "Mapping out a Future for Ungulate Migrations." *Science* 372(6542): 566–9. https://doi.org/10.1126/science.abf0998

Mallon, D. P. 2008. "*Procapra gutturosa*, The IUCN Red List of Threatened Species 2008." e.T18232A7858611.

Muñoz Sabater, J. 2019. "ERA5-Land Monthly Averaged Data from 1981 to Present." *Copernicus Climate Change Service (C3S) Climate Data Store (CDS)*. https://doi.org/10.24381/cds.68d2bb3.

Nandintsetseg, D., C. Bracis, P. Leimgruber, P. Kaczensky, B. Buuveibaatar, B. Lkhagvasuren, and T. Mueller. 2019. "Variability in Nomadism: Environmental Gradients Modulate the Movement Behaviors of Dryland Ungulates." *Ecosphere* 10(11): e02924. https://doi.org/10.1002/ecs2.2924

Nandintsetseg, D., C. Bracis, K. A. Olson, K. Böhning-Gaese, J. M. Calabrese, C. Buyanaa, and T. Mueller. 2019. "Challenges in the Conservation of Wide-Ranging Nomadic Species." *Journal of Applied Ecology* 56(8): 1916–26. https://doi.org/10.1111/1365-2664.13380

Olson, K. A., T. Mueller, S. Bolortsetseg, P. Leimgruber, W. F. Fagan, and T. K. Fuller. 2009. "A Mega-Herd of More than 200,000 Mongolian Gazelles *Procapra gutturosa*: A Consequence of Habitat Quality." *Oryx* 43(1): 149–53. https://doi.org/10.1017/S0030605307002293

Stratmann, T. S. M., N. Dejid, J. M. Calabrese, W. F. Fagan, C. H. Fleming, K. A. Olson, and T. Mueller. 2021. "Resource Selection of a Nomadic Ungulate in a Dynamic Landscape." *PLoS One* 16(2 Febuary): 1–25. https://doi.org/10.1371/journal.pone.0246809

Teitelbaum, C. S., and T. Mueller. 2019. "Beyond Migration: Causes and Consequences of Nomadic Animal Movements." *Trends in Ecology & Evolution* 34(6): 569–81. https://doi.org/10.1016/j.tree.2019.02.005

Zhaowen, J., S. Takatsuki, G. Zhongxin, and J. Kun. 1998. "The Present Status, Ecology and Conservation of the Mongolian Gazelle, *Procapra gutturosa*: A Review." *Mammal Study* 23: 63–78. https://doi.org/10.3106/mammalstudy.23.63

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Dejid, Nandintsetseg, Kirk Olson, Theresa S. M. Stratmann, and Thomas Mueller. 2022. "A Gazelle's Extraordinary, 18,000-km-Long Journey through the Steppes of Mongolia." *Ecology* 103(5): e3660. https://doi.org/10.1002/ecy.3660