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Variability in nomadism: environmental gradients modulate the movement behaviors of dryland ungulates

Dejid Nandintsetseg[1,2,3,†] Chloe Bracis[1,2,4] Peter Leimgruber,[3] Petra Kaczensky[5,6] Bayarbaatar Buuveibaatar[7] Badamjav Lkhagvasuren,[8] Buyanaa Chimeddorj,[9] Shiilegdamba Enkhtuvshin,[7] Ned Horning,[10] Takehiko Y. Ito,[11,12] Kirk Olson,[7] John Payne,[7] Chris Walzer[6,7] Masato Shinoda,[13] Jared Stabach,[3] Melissa Songer,[3] and Thomas Mueller[1,2,3]

[1]*Senckenberg Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, 60325 Frankfurt (Main), Germany*
[2]*Department of Biological Sciences, Goethe University Frankfurt, 60438 Frankfurt (Main), Germany*
[3]*Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal Virginia 22630 USA*
[4]*Ifremer, Channel and North Sea Fisheries Research Unit, Boulogne-sur-Mer, France*
[5]*Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway*
[6]*Research Institute of Wildlife Ecology, University of Veterinary Medicine, Vienna, Vienna A-1160 Austria*
[7]*Mongolia Program, Wildlife Conservation Society, Ulaanbaatar, Mongolia*
[8]*Institute of General and Experimental Biology, Mongolian Academy of Sciences, Ulaanbaatar 13330 Mongolia*
[9]*Mongolia Program Office, World Wide Fund for Nature, Ulaanbaatar, Mongolia*
[10]*American Museum of Natural History's Center for Biodiversity and Conservation, New York, New York, USA*
[11]*Arid Land Research Center, Tottori University, Tottori 680-0001 Japan*
[12]*Organization for the Strategic Coordination of Research and Intellectual Properties, Meiji University, Tokyo 168-8558 Japan*
[13]*Graduate School of Environmental Studies, Nagoya University, Nagoya 464-8601 Japan*

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Abstract. Studying nomadic animal movement across species and ecosystems is essential for better understanding variability in nomadism. In arid environments, unpredictable changes in water and forage resources are known drivers of nomadic movements. Water resources vary temporally but are often spatially stationary, whereas foraging resources are often both temporally and spatially variable. These differences may lead to different types of nomadic movements: forage- vs. water-driven nomadism. Our study investigates these two different types of nomadism in relation to resource gradients from mesic steppe to xeric desert environments in Mongolia's Gobi-Steppe Ecosystem. We hypothesized that in the desert, where water is a key resource, animals are more water-dependent and may show water-driven nomadism with frequent revisits to spatially fixed resources, while in the steppe, animals are less water-dependent and may show forage-driven nomadism, tracking high-quality foraging patches with infrequent revisits to previously used resources. We utilized GPS movement data from 40 individuals of four ungulate species (Mongolian gazelle, goitered gazelle, saiga antelope, and Asiatic wild ass) in the Gobi-Steppe Ecosystem. We calculated displacement distances and recursion metrics and subsequently performed a principal component analysis to quantify the variation in movement patterns. The satellite-derived vegetation greenness served as a proxy for the resource gradient and was associated with variation in movement behaviors described by the first principal component, demonstrating that the variability in movements was closely related to the resource gradient from mesic to xeric habitats. We showed that ungulates in the resource-rich steppe tended to move long distances with few revisits (forage-driven nomadism), while ungulates in the resource-poor desert tended to move shorter distances with more revisits (water-driven nomadism). Our results suggest that xeric and mesic habitats promote different types of nomadic strategies. These results have important implications for conservation strategies: Forage-driven nomads primarily require a high degree of landscape-level permeability, and water-driven nomads additionally require the protection of ephemeral water bodies and actions to maintain the functional connectivity between them.

Key words: animal movement; arid; forage; nomadism; recursion; resource; ungulate; water.

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† **E-mail:** nandintsetseg.dejid@senckenberg.de

Introduction

In resource-poor arid environments where precipitation is stochastic, nomadic movement is a common strategy employed by animals to cope with the unpredictable changes in resource availability (Dean 2004, Jonzén and Knudsen 2011). Characterized by non-seasonal and irregular movements, nomadism occurs across a variety of taxa, including amphibians (Plotkin 2010), birds (Robillard et al. 2018), carnivores (Mauritzen et al. 2001), marine animals (Quinn and Brodeur 1991), and large herbivores (Tear et al. 1997).

Though nomadism is relatively little studied, recognized drivers of nomadic movements include unpredictable spatiotemporal changes in resource distribution and extreme climatic events, including droughts, severe winters, and flooding rains that result in resource pulses (Kaczensky et al. 2011*a*, Greenville et al. 2012, Szymkowiak and Kuczyński 2015, Jordan et al. 2017). The most commonly observed driver of nomadic movement is unpredictable changes in ephemeral resources, such as water or forage, where animals tend to move long distances to track broadscale patchy resources (Fryxell et al. 2004, Roshier et al. 2008). In arid environments, key resources are water and forage, which are often temporally variable, but can be static or dynamic in their locations. In deserts and semideserts, water is often a key resource and animals have to drink regularly or rely on foraging resource derived from water availability. Water availability at ephemeral oases and wetlands is temporally unpredictable, but their spatial location is often relatively static. These unpredictable changes in the water availability could lead to water-driven nomadism. For example, the gray teal *Anas gracilis* in Australia, a nomadic waterbird, moves long distances to track high food abundance in response to infrequent wetland flooding events (Roshier et al. 2008). In contrast, ephemeral, broadscale foraging patches can drive forage-driven nomadism, where animals track broadscale patches containing suitable food resources. Their spatial location may depend less on topographic features but more on ephemeral rainfall events, and consequently, the spatial location of suitable foraging patches may be far less predictable. For example, swift parrots *Lathamus discolor,* a nectarivorous species in Australia, follow the erratic flowering of black and blue gum trees (Webb et al. 2014). The variability in nomadic movement patterns has not received much attention in the literature. This is especially true for nomadic ungulates, where a lack of adequate movement data has made comparisons between species and ecosystems difficult. Such comparisons and research are essential to improve our understanding of variability in nomadism and its ecological consequences.

The Gobi-Steppe Ecosystem in Mongolia provides a unique opportunity to explore differences in resource-driven nomadism across a suite of ungulate species characterized by their wide-ranging movements (Batsaikhan et al. 2014). The Gobi-Steppe Ecosystem is an arid region, which consists of a gradient, ranging from the herbaceous steppe covering eastern Mongolia (mesic habitat with annual precipitation of about 300 mm) to the drier and shrubbier Gobi Desert and semidesert covering southern and southwestern Mongolia (xeric habitat with annual precipitation ranging from 50 mm up to 200 mm; Kottek et al. 2006, Chimed-Ochir et al. 2010). Both the mesic steppe and xeric desert are characterized by variable rainfall in space and time (Khishigbayar et al. 2015, Vandandorj et al. 2015). The Gobi-Steppe Ecosystem supports the largest populations of Mongolian gazelle *Procapra gutturosa*, Asiatic wild ass (or khulan in Mongolian) *Equus hemionus*, goitered gazelle *Gazella subgutturosa*, and a subspecies of saiga antelope *Saiga tatarica mongolica* (Young et al.

2010, Batsaikhan et al. 2014, Buuveibaatar et al. 2016*b*; Fig. 1). In the mesic steppe, ungulates (such as Mongolian gazelle) can track unpredictable patches of high-quality green vegetation (Mueller et al. 2008, 2011). In contrast, ungulates in deserts seem to be more dependent on spatially explicit water sources that are often spaced far apart, promoting high mobility of ungulates (Kaczensky et al. 2010, Nandintsetseg et al. 2016).

Here, we compiled GPS movement data from each of the four ungulate species above to examine variability in their nomadic movement behaviors along an ecological gradient from mesic steppe to xeric desert in the Gobi-Steppe Ecosystem. We used movement metrics, including displacement distances and recursion metrics, which have previously been useful in classifying broadscale movement patterns (Abrahms et al. 2017). Our aim was to gain a better understanding of how nomadic movements in drylands vary across ungulate species and environments. We hypothesized that desert ungulates, which usually rely on water sources to meet their water needs, will exhibit water-driven nomadism. That is, movements of ungulates should be constrained by water sources and they should return frequently to previously visited areas in relatively short intervals. In contrast, in the more vegetated steppe, ungulates likely meet their water needs from high-quality green vegetation. Thus, we expect that in these landscapes, ungulates will show forage-driven nomadism with long-distance movements, few revisits, and longer revisit intervals.

Materials and Methods

Study species and region

The Gobi-Steppe Ecosystem in Mongolia covers an area of 827,000 km^2 across eastern, southern, and southwestern Mongolia (Batsaikhan

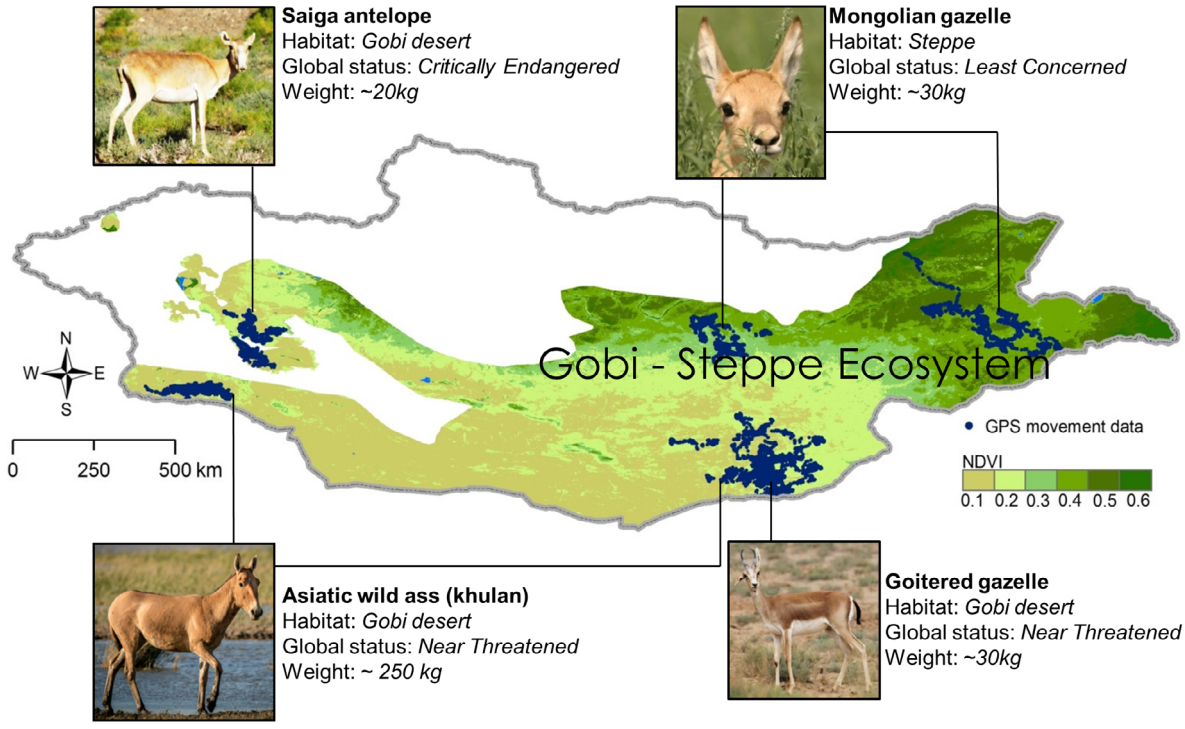

Fig. 1. The joint distribution range of wide-ranging ungulates occupying the Gobi-Steppe Ecosystem in Mongolia. The distribution range for each species is derived from IUCN assessments. GPS movement dataset from the four study species is highlighted in blue. The background image shows the distribution of 12-yr average of vegetation greenness (Normalized Difference Vegetation Index [NDVI] from 2006 to 2017) for summer months (April–October).

et al. 2014) and encompasses the distribution range of our four study species (Fig. 1). In this arid and semiarid ecosystem, high spatial and temporal variability in precipitation drives highly variable forage and water availability over time (Fernandez-Gimenez and Allen-Diaz 1999, Vandandorj et al. 2015).

The east of the Gobi-Steppe Ecosystem is characterized by flat steppe and rolling hills, whereas the south and southwest are characterized by semidesert and desert ecosystems. The elevation in the eastern steppe ranges from 800 to 1300 m, increasing to 1800 m in the southern Gobi Desert (Kaczensky et al. 2011*b*, Buuveibaatar et al. 2013, Imai et al. 2017).

The steppe is characterized by a cold steppe climate with a lack of surface water and average annual precipitation of 300 mm (Kottek et al. 2006). Plant communities are primarily herbaceous with *Stipa krylovii*, *Stipa grandis*, *Carex duriuscula*, and *Cleistogenes spp*. Local herders use hand-drawn wells, and wild animals rely on high-quality green vegetation during the warm, growing season. The eastern steppe provides critical habitat for about one million Mongolian gazelle, the largest population in the world (Mallon 2008).

The Gobi Desert is characterized by a cold desert climate, and average annual precipitation ranges from 50 mm up to 200 mm (Kottek et al. 2006, Kaczensky et al. 2011*b*). The Gobi Desert is an open shrubland where vegetation is sparse with barren ground. Plant communities are characterized by xerophytic shrubs (e.g., *Caragana spp*, *Haloxylon ammodendrum*, *Artemisa* spp), xerophytic herbs and grasses (e.g., *Stipa gobica*), and perennial forbs (e.g., *Allium polyrhizum*). Water sources are sparsely distributed, occurring in the form of springs, which sometimes form short rivers and oases, as well as ephemeral basins and drainages. With an estimated 40,000 khulan and 30,000 goitered gazelle, the Mongolian Gobi Desert supports the largest remaining population of khulan and goitered gazelle in the world (Buuveibaatar et al. 2016*b*). In addition, the Gobi Desert sustains a small population of a distinct subspecies of the critically endangered saiga antelope (IUCN SSC Antelope Specialist Group 2018).

GPS movement data

We compiled GPS movement data for four ungulate species: Mongolian gazelle in the steppe and khulan, goitered gazelle, and saiga antelope in the desert. Tracking periods ranged from 2006 to 2017, and the recording intervals between GPS fixes varied from every 15 min to every 4–5 h.

To standardize movement data across individuals, we resampled all data to a 4-h interval except for three individual saiga antelope that were sampled at a 5-h interval (Appendix S1: Table S1). Given our research interest in forage- vs. water-driven nomadism, we focused on movement data collected in the warm, vegetation growing season and we excluded the cold non-growing season. Although the growing season lasts from April to October, we used a 4-month window from April to July, which has the highest greenness, because some saiga antelope and khulan individuals lacked movement data from August to October. The final dataset included 27,368 GPS positions over 4 months for 11 Mongolian gazelle, six goitered gazelle, 15 khulan, and eight saiga antelope, with datasets ranging from 539 to 732 GPS locations (Appendix S1: Table S1). Overall, the total number of GPS locations for saiga antelope was slightly less than for the other species due to a 5-h sampling interval for three individuals and a lack of recorded movement data for five individuals at the end of the tracking period.

Movement metrics

We calculated five movement metrics for each individual to evaluate the variability of nomadic behavior across the four species. The movement metrics included displacement distances at two different timescales and three recursive movement metrics.

Displacement distances.—We calculated 1-d and 10-d displacement distances for each individual using the move R package (Bart et al. 2018). The 1-d displacement (hereafter daily displacement) was calculated as the distance between two consecutive GPS positions 24 h apart except for the three individual saiga antelope where locations were 25 h apart. We were also interested in the displacement over longer time frames. Following Tucker et al. (2018), we additionally calculated the 10-d displacement as the distance between two consecutive GPS positions 10 d apart.

Recursive movement metrics.—Recursive movement metrics (e.g., repeated movements to previously visited areas) have been used as a useful

proxy for repeated use of specific areas (Berger-Tal and Bar-David 2015), in particular for identifying revisits to high-quality foraging patches by large herbivores (Benhamou and Riotte-Lambert 2012, Giotto et al. 2015) and for classifying movement patterns across vertebrate taxa (Abrahms et al. 2017). For each individual, we calculated three recursive movement metrics, revisit rate, residence time, and return time, using the recurse R package (Bracis 2018, Bracis et al. 2018). Revisit rate is defined as the total number of visits to previously visited locations within a defined radius, residence time is defined as the total amount of time an individual spends inside a defined radius across all visits, and return time is the amount of time elapsed between visits (Bracis et al. 2018).

We calculated these metrics for each GPS location along the movement trajectory. We defined a 1 km circle radius based on median step lengths across species centered on the focal GPS location. Step length was calculated as the Euclidean distance between consecutive GPS locations at a 4-h interval, and the median step length was 0.79 ± 1.55 km (median ± standard deviation [SD]) for Mongolian gazelle, 0.73 km ± 1.22 km for goitered gazelle, 0.96 ± 1.81 km for saiga antelope, and 1.20 ± 2.31 km for khulan, respectively (Appendix S1: Fig. S1). The median step length across all species was ~1 km, leading us to select a radius of 1 km. We then set a threshold time of 8 h to eliminate brief excursions outside the defined radius, but to capture more significant return movements, for example, to drink or forage. Therefore, recursions were identified when an individual left a radius of 1 km and then returned after a period of more than 8 h to the same area. We additionally confirmed the appropriateness of a 1 km radius by conducting a sensitivity analysis using different radii from 0.1 to 5 km in increments of 0.1 km (Appendix S1: Fig. S2) and threshold times of 4, 8, and 12 h (Appendix S1: Fig. S3). Eventually, the number of revisits started to decrease at a radius of 2 km, indicating that the radius is too large to be at a scale of ecological interest. Recursion patterns across species were consistent across thresholds of 4 and 12 h (Appendix S1: Figs. S3, S4).

We calculated mean daily and 10-d displacement distances, mean recursion rate, mean residence time, and mean return time for each individual in order to compare movement metrics across species. We then performed one-way analysis of variance (ANOVA) tests with each of the five movement metrics as the response variable and species as the predictor variable to determine whether there are any statistically significant differences in the movement metrics between the four species (Appendix S1: Table S2). Next, we used the Tukey honest significant difference (Tukey HSD) test to determine which pairs of species were significantly different from each other in the case that the ANOVA result was significant using the TukeyHSD function in the stats package (R Core Team 2019).

Ordination analysis

Because most movement metrics were correlated, we performed a principal component analysis (PCA) for the five movement metrics using the prcomp function in the stats R package (R Core Team 2019) to explore any underlying patterns in the movement metrics across species. All movement metrics were first log-transformed. To choose which PCA axis best explained our dataset, we used the broken-stick criterion, in which components are retained if their eigenvalues exceed those expected from random data (Peres-Neto et al. 2003). For the subsequent analysis, we selected the first principal component (PC1), which explained 72.9% of variation in the empirical dataset (see *Results* for details; Fig. 3).

Foraging resource availability

We used Normalized Difference Vegetation Index (NDVI) as a proxy for vegetation availability to examine whether the gradient from the more mesic steppe to the xeric desert explained any of the variability in movement behavior detected in the PCA. The NDVI data were obtained from the 16-D 250-m MODIS NDVI product (MOD17A3, version 055; https://lpdaacsvc.cr.usgs.gov/appeears/) from April to July for the years 2006 to 2017, the period in which our GPS movement data were collected, resulting in 95 composite images. For each pixel, we calculated the mean of NDVI across the 95 composites, indicating the 12-yr average vegetation availability between April and July across the Gobi-Steppe Ecosystem. We annotated GPS locations with the mean NDVI value for that pixel and then averaged values for each

individual. We used linear mixed-effects models using lme4 R package (Bates et al. 2015) to predict the relationship between the NDVI gradient as the independent variable and the variability in movement behavior detected in the PC1 as the dependent variable. Species was included in the model as a random intercept. Because we only had one species in mesic habitat (Mongolian gazelle), we also tested the model by excluding Mongolian gazelle to determine whether we could also find a relationship between the NDVI gradient and the variability in movement behavior over the smaller range of NDVI values found in xeric habitat. The marginal r^2, representing the total variance explained by the fixed effects, was calculated using the r.squaredGLMM function in the MuMIn R package (Barton 2018). All analyses were conducted using R 3.5.0 (R Core Team 2019).

Results

Variability of movement behavior across ungulate species

We found significant differences in the movement metrics across species (Fig. 2a–e; Appendix S1: Table S2).

For daily displacement, goitered gazelle in the desert had the shortest daily displacement (2.3 ± 0.8 km; mean ± SD), significantly shorter than any of the other three species (Fig. 2a; Appendix S1: Table S2). Khulan in the desert had the longest mean daily displacement (7.0 ± 1.3 km), significantly greater than both Mongolian gazelle (4.6 ± 1.4 km) in the steppe and saiga antelope (4.9 ± 1.2 km) in the desert, which were not significantly different from each other (Fig. 2a).

For 10-d displacement, the longer timescale, goitered gazelle had the shortest displacement (7.9 ± 7.2 km), which was not significantly different from those of saiga antelope (14.0 ± 6.9 km; Fig. 2b; Appendix S1: Table S2). In comparison, Mongolian gazelle and khulan both moved longer distances (20.9 ± 10.4 km and 31 ± 8.7 km, respectively), which were not significantly different from each other. The mean 10-d displacement of khulan was over four times longer than goitered gazelle and two times longer than saiga antelope, and that of Mongolian gazelle was three times greater than goitered gazelle (Fig. 2b; Appendix S1: Table S2).

For revisit rate, goitered gazelle had a mean revisit rate of 17.8 ± 14.6 times (mean ± SD) that was significantly greater than any of the other species. Mongolian gazelle had the lowest mean revisit rate (3.6 ± 3.2), but this was not significantly lower than khulan (5.5 ± 5.9) and saiga antelope (6.6 ± 5.9), which did not significantly differ from each other (Fig. 2c; Appendix S1: Table S2).

For residence time, there was a similar pattern as revisit rate (Fig. 2d; Appendix S1: Table S2). Due to the frequent revisits, goitered gazelle had a long mean residence time of 12.0 ± 6.8 d (mean ± SD) in specific areas. In contrast, Mongolian gazelle had a mean residence time of 1.9 ± 1.6 d, which was not significantly different from khulan (4.6 ± 5.8) and saiga antelope (4.6 ± 3.9).

The return time showed no significant differences among species. The mean return time was 3.0 ± 1.4 d (mean ± SD) for goitered gazelle, 4.7 ± 2.8 d for saiga antelope, 4.2 ± 1.9 d for khulan, and 5.8 ± 2.8 d for Mongolian gazelle (Fig. 2e; Appendix S1: Table S2).

The first two principal components (PCs) of these movement metrics explained 91.0% of the variance among the movement metrics for the four ungulate species (Table 1, Fig. 3). The first PC (hereafter PC1) explained 72.9% of the variance, representing the largest variation among the movement metrics, and was positively correlated with revisits and residence time and negatively correlated with daily and 10-d displacement distance (Table 1, Fig. 3). The second PC (PC2) explained 18.1% of the variance and was positively correlated with return time (Table 1, Fig. 3). For increasing values along the PC1 axis, there was a change from long-distance movements with infrequent revisits to short-distance movements with frequent revisits. In contrast, along the PC2 axis individuals mainly varied in their return time. For the subsequent analysis, we selected PC1 to investigate the relationship between the variability in movement behavior across species and a gradient of resource availability.

Variability in movement behavior in relation to the availability of vegetation

The linear mixed-effects model showed vegetation availability (NDVI) was a significant

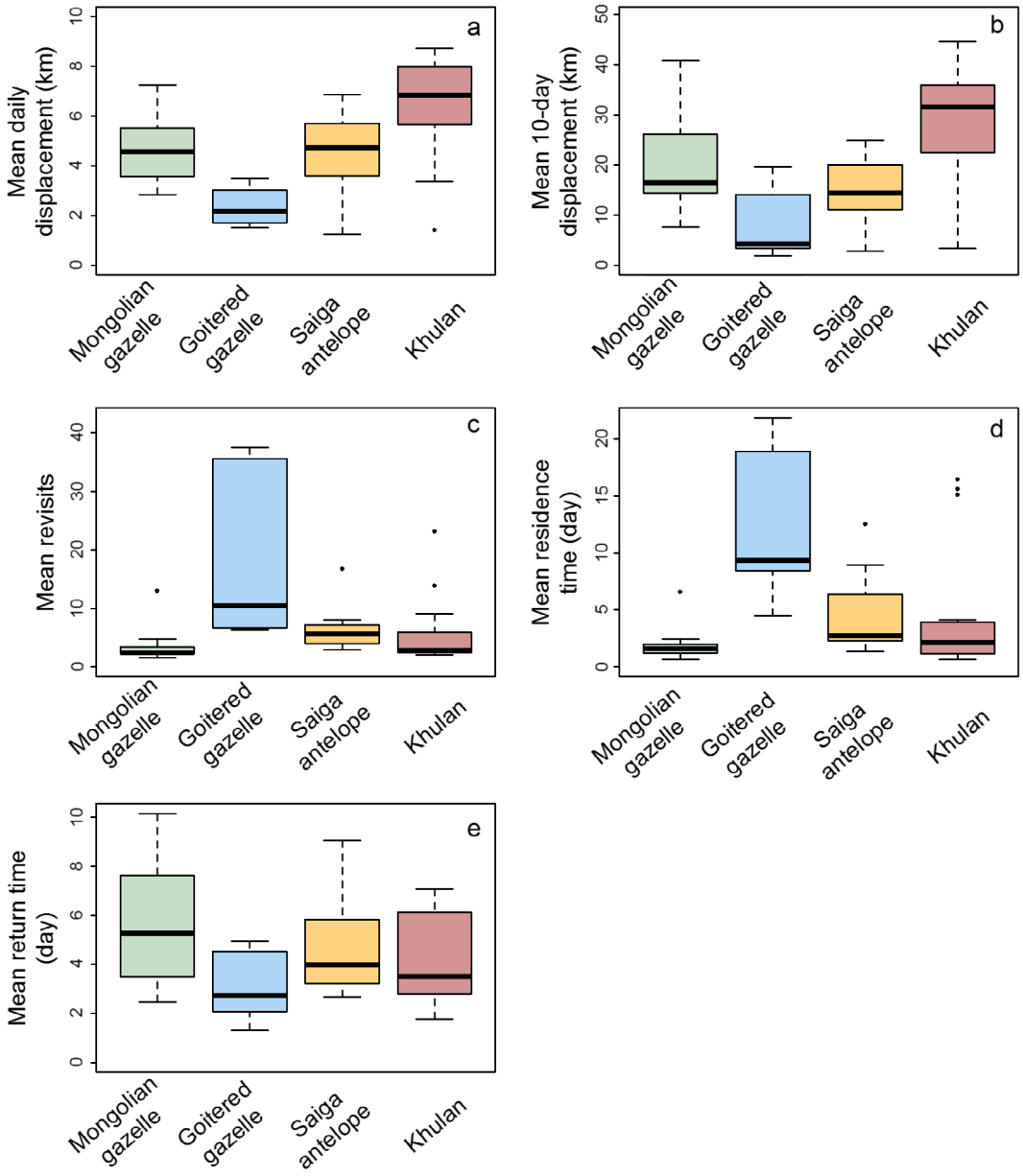

Fig. 2. Movement metrics of four ungulate species in the Gobi-Steppe Ecosystem in Mongolia. The movement metrics showed that khulan living in the desert and Mongolian gazelle living in the steppe were the most similar to each other (Appendix S1: Table S2). They had longer displacement distances and fewer revisits. Goitered gazelle living in the desert had the shortest displacement distances, the highest number of revisits, and the longest residence time. In contrast, saiga antelope, also living in the desert, was intermediate to the movements of other species included.

predictor of the variability of nomadic movement behavior (PC1), explaining approximately 21% of the variance in PC1 of the movement metrics (Fig. 4; Appendix S1: Table S3). The coefficient estimate for NDVI was negative, indicating that in more vegetated mesic habitats, individuals moved longer distances and returned less frequently to previously visited areas. In contrast,

Table 1. Contributions of movement metrics and cumulative percentage of variance explained by each principal component (PC).

Movement metrics	PC1	PC2	PC3	PC4	PC5
	−0.48	−0.09	0.61	−0.29	−0.54
10-d displacement	−0.49	−0.2	0.33	0.26	0.72
Revisits	0.49	0.008	0.41	−0.65	0.38
Residence time	0.48	0.08	0.57	0.64	−0.13
Return time	−0.19	0.97	0.07	−0.02	0.11
Cumulative percentage	72.9	91.0	97.3	99.1	100

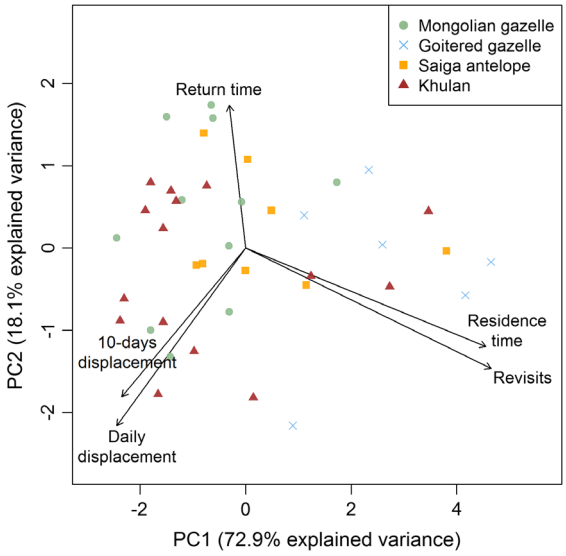

Fig. 3. Relationship of movement metric PC1 and PC2 for each individual.

in less vegetated xeric desert habitats, individuals moved shorter distances with more frequent revisits to previously visited areas (Fig. 4). This relationship still held when Mongolian gazelle were excluded from the model (Appendix S1: Table S4), indicating that this pattern exists across species and is not driven solely by the response of Mongolian gazelle to the greater variation in the resource gradient in mesic habitats.

Discussion

Our results showed two different behaviors of nomadic ungulate movements in the Gobi-Steppe Ecosystem. The behaviors varied between long-distance movements with infrequent revisits and short-distance movements with frequent revisits to previously visited areas (Fig. 3). This variability was partially explained by the gradient of vegetation availability in the ecosystem (Fig. 4). In the mesic steppe, with greater vegetation availability, nomadic movement behavior was characterized by longer movements with infrequent revisits to previously used areas (Fig. 4). In contrast, in the desert, the movement behavior was characterized by shorter distances and more frequent revisits. Overall, this pattern supports our initial hypothesis differentiating forage-driven nomadism, tracking broadscale and spatially unpredictable foraging resource in the mesic steppe, from water-driven nomadism in xeric deserts where animals tend to revisit ephemeral but spatially fixed water bodies.

These results are somewhat contradictory to macro-ecological research on animal movements that links resource availability to migration distances of large herbivores and shows in

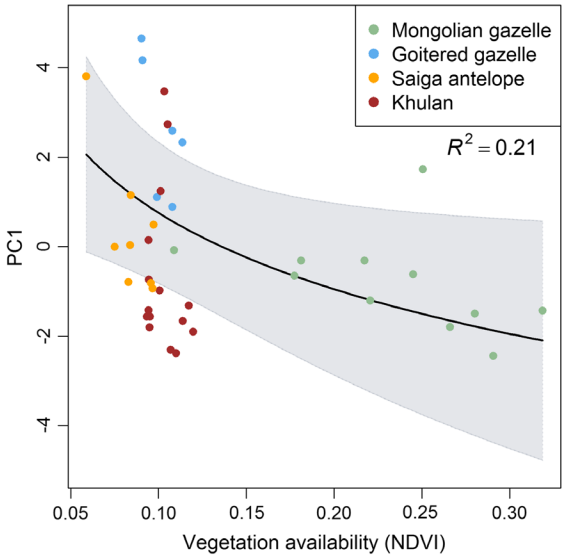

Fig. 4. The relationship between nomadic movement behavior and a gradient of vegetation availability in the Gobi-Steppe Ecosystem. The gray area represents the 95% confidence interval for the predicted values. PC1 characterizes the movement behavior from long-distance movements with few revisits to short-distance movements with high revisits to previously visited areas.

resource-poor arid environments, animals move longer distances than animals in resource-rich environments (Teitelbaum et al. 2015, Tucker et al. 2018). These macro-ecological studies, however, usually cover a broad gradient from forest to temperate grasslands, while our comparative study of nomadic ungulates focused specifically on arid environments from herbaceous mesic steppes to shrubby xeric deserts. Along this resource gradient in arid environments, animals in deserts seem to reverse the general pattern found in the macro-ecological research (i.e., longer movements in more arid regions), with animals moving longer distances in more mesic habitats (Fig. 2). Mongolian gazelle in the mesic steppe with more vegetation, for instance, moved nearly three times further than similar-sized goitered gazelle in the xeric desert at a 10-d scale. This indicates that in the resource-rich mesic steppe, nomadic ungulates might be able to afford moving long distances without a need to return to previously visited areas. This pattern might be linked to highly dynamic foraging resources, which are spatially variable and temporally unpredictable in combination with independence from water sources, thus allowing free movements.

Evidence from theoretical and empirical research demonstrates the importance of landscape structure to animal movements. For instance, landscapes where resources are spatially variable and temporally unpredictable generally lead to long-distance nomadic movements and low landscape persistence (Mueller and Fagan 2008, Fagan et al. 2013). A multi-species comparative study of ungulate movements across different landscapes highlighted that the long-distance nomadic movements are triggered by increasing unpredictability in green vegetation (Mueller et al. 2011). Other studies of large herbivores have also found that animals move faster in more heterogeneous landscapes to increase encounters with foraging areas (Avgar et al. 2013). Additionally, simulation models have suggested that random search strategies favor encounter success in patchy and aggregated foraging resources (Raposo et al. 2011). The fact that Mongolian gazelle exhibited infrequent visits to previously visited areas may indicate that they perform random searches to increase encounter rates of high-quality foraging areas in the mesic steppe.

In the resource-poor xeric deserts, ungulate movements were characterized by shorter movements and high repeated use of resources (but see the discussion of species-specific differences and the exceptional long movements of khulan). This movement pattern might be related to the fact that animal movements in xeric habitats are mostly constrained by surface water availability (Giotto et al. 2015, Martin et al. 2015). In many ecosystems, water resources have long been recognized as a fundamental need for large herbivores and have been considered as critical places where animals must return periodically, resulting in constrained movements for water-dependent species (Bleich et al. 2010, Rozen-Rechels et al. 2015). For example, feral horses in Sable Island National Park in Canada were located close to water sources in summer (Rozen-Rechels et al. 2015), and the distribution of waterbuck in Kruger National Park in South Africa was constrained by surface water availability (Redfern et al. 2003). Numerous studies have shown that animals access forage further away from water sources until they have to return to water, resulting in a commuting pattern between forage and water resources. A recent study on effects of spatial memory on movement decisions has demonstrated that wide-ranging elephants in African savanna showed highly directional rapid movements to the closest water sources, indicating a detailed spatial memory allowing them to minimize travel distance to water resources (Polansky et al. 2015). In the xeric Gobi Desert, a previous study suggested return movements of khulan to sparsely distributed small springs and large oases, whose locations are spatially static, but availability of water at these locations is temporally unpredictable (Nandintsetseg et al. 2016). While our findings generally support the notion that an environmental gradient from mesic to xeric habitats modulates return movements, we emphasize that due to our broadscale study region with sparsely distributed ephemeral water sources, we were not able to validate that recursive movements were indeed to waterbodies.

Remarkably, movement metrics showed significant variability among species even within the xeric desert environment (Fig. 2). In particular, goitered gazelle had the highest mean revisits and residence time and the shortest displacement distance for both daily and 10-d displacements,

suggesting goitered gazelle return often to only a few specific areas. By comparison, saiga antelope, a similar-sized ungulate in the desert, was more mobile and showed fewer return movements to areas used previously. This difference between goitered gazelle and saiga antelope in the desert suggests that goitered gazelle could be more water-dependent than saiga antelope. Although several studies reported that water is an important resource for saiga antelope (Bekenov et al. 1998, Singh et al. 2010), water usage and its effects on their movements has been little studied. However, we note that saiga antelope individuals had fewer GPS locations (539–583 locations) than goitered gazelle did (659–732 locations). The smaller sample size could have potentially affected the recursion movement metrics. On the other hand, the displacement distances showed that saiga antelope move longer distances than goitered gazelle, indicating that saiga antelope likely return to previously visited areas less than goitered gazelle and supporting the results of the recursion analysis.

The movement behavior of khulan was characterized by very long movement distances, and few revisits to previously used areas, indicating khulan are highly mobile. Khulan, an equid species, is dependent on more or less daily access to water sources, and distance to water is an essential factor in habitat use (Kaczensky et al. 2010, Buuveibaatar et al. 2016*a*, Nandintsetseg et al. 2016). However, khulan are capable of accessing water by digging in dry riverbeds, where the groundwater table is high (Feh et al. 2001), which in some areas could potentially make them less dependent on permanent surface water. In addition, khulan are a large-bodied (~250 kg), non-ruminant ungulate species, which tend to move longer distance than smaller ungulates and are adapted to process large quantities of low-quality forage (Senft et al. 1987, Duncan et al. 1990). Together, these factors may explain the high mobility of khulan in the desert. In contrast, goitered gazelle are a medium-sized (~30 kg), ruminant ungulate, which rely on high-quality forage (Senft et al. 1987, Duncan et al. 1990) and they likely rely on permanent water sources because they are unable to access the groundwater via excavation. Future research could examine whether goitered gazelle can follow the movements of khulan to access ephemeral water sources in areas where both species coexist.

Overall, we emphasize that the coarse sampling rate (4-h interval GPS fixes) and the four-month GPS movement dataset could have reduced the detection of recursive movements. Animals might require more water or patches with high-quality water-rich green vegetation in August through October when vegetation becomes drier, but data were not available for all four species during these months. Differences in recursive patterns might be more pronounced with more fine scale and longer term data.

Several aspects of our research could be improved upon in future studies. While our study uses the most comprehensive dataset on nomadic ungulates species we are aware of, a longer term and higher resolution dataset on movements of nomadic ungulate species would be helpful to better detect spatiotemporal patterns in the variability of movements and to develop conservation strategies. This would also allow researchers to examine whether nomadic animals use long-term memory and return to previously visited areas between multiple years. It would also enable understanding whether nomadic ungulates reuse refuge areas during extreme climatic events, such as is observed in nomadic birds (Runge et al. 2016). With our current movement dataset of four ungulate species, it was impossible to test long-term return movements (e.g., seasonal and/or between-year returns) and to examine short- and long-term spatial memory. Additionally, future studies could increase the number of individuals and species to the dataset. In particular, for the mesic steppe environment, Mongolian gazelle was the only species available. Future research examining additional individuals and species under mesic conditions would help to corroborate the pattern found here. Such studies could build more complex models including interaction terms between NDVI and species or random slope and intercept models and could consider additional effects such as resource heterogeneity, resource predictability, resource recovery rate, seasonal and annual variability in resources, and animals' cognitive capabilities on recursion movements (Berger-Tal and Bar-David 2015). Finally, there are a number of additional factors that potentially influence recursion movement

metrics that we did not investigate here. These include predator avoidance, resting sites, social structure, and human-induced disturbance (Montpellier and Centre 2008, Benhamou and Riotte-Lambert 2012, English et al. 2014).

Conclusion

Our study is one of the first to compare movements of nomadic ungulates across a resource gradient and across species in an arid environment, contributing to a better understanding of the variability of nomadic movements across species and ecosystems. Overall, our study suggests that in arid and semiarid ecosystems, nomadic movement behavior may differ across resource gradients. In the resource-rich mesic steppe with temporally unpredictable foraging resources, animals can afford exceptional long-distance movements and make less repeated use of specific areas. In contrast, in the resource-poor xeric desert, where a main driver of nomadic movements is ephemeral but spatially fixed water resources, movements are constrained, and animals exhibit more repeated use of specific areas. Importantly, our findings have significant implications for developing conservation strategies: For forage-driven nomads with few revisits to previously visited areas, permeability across the entire landscape is a key requirement. For water-driven nomads, in addition to landscape permeability, conservation should focus on water bodies and connectivity among sparsely distributed and temporally unpredictable water resources.

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