

**NOMADIC ANIMAL MOVEMENTS AND THEIR
CONSERVATION CHALLENGES**

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In Loving Memory of my Brother

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1 SUMMARY

Recent studies on movement ecology have shown that in resource-poor arid regions, large mammalian herbivores tend to perform nomadic, long-range movements rather than seasonal migrations. Some studies have associated these nomadic movements with the spatially variable and temporally unpredictable foraging resources at the landscape scale. While migration is well studied, there are very few case studies for nomadic ungulates regarding the drivers of their movements and the variability in movement patterns. In addition, numerous studies have indicated that a key challenge in conserving highly mobile species lies in the need to accommodate the unpredictable nature of their long-distance movements. Conservation measures that have been developed for migrants, such as the conservation of migration corridors or calving- or wintering grounds, will not work for nomads when movements are unpredictable.

The overarching aim of my doctoral research was to examine and quantify the spatiotemporal variability in the movements of nomadic ungulates to better understand the possible drivers and characteristics of such movements as well as to examine the particular conservation challenges associated with nomadic movements. In this thesis, I developed a conceptual framework focusing on the key characteristics of nomadic movements to investigate three main research objectives: (i) the environmental drivers of nomadic movements, (ii) the temporal dynamics of space use, and (iii) the variability in nomadic movement behavior across ungulates and ecosystems. Furthermore, I linked the main findings to existing conservation concepts for highly mobile species and provided a closing synthesis. The findings of my research contribute towards the future development of conservation concepts for nomadic species, which is essential for the continued existence of nomadism and preserving the movement as a behavioral phenomenon.

For the first research objective, I used a long-term ground-based line transect wildlife dataset that includes data on the Asiatic wild ass (khulan in Mongolian) *Equus hemionus*, which was compiled by researchers and rangers associated with the Great Gobi B Protected Area in Mongolia. I investigated whether spatiotemporal dynamics of the foraging habitat of khulan, a highly mobile ungulate species, are indeed the most likely driver of their nomadic movements. Main results point towards temporal dynamics of water availability rather than dynamics in foraging habitat may be the main driver for exceptional long-range movements of khulan in the Gobi desert. This main finding provides new insights in the underlying causes of one of the least

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understood movement patterns and also further increases our understanding of spatiotemporal drivers for nomadic movements.

For the second objective, I used a multiple-year GPS movement dataset I collected together with colleagues on the Mongolian gazelle *Procapra gutturosa* in Mongolia's steppe. I examined the variability in space use of Mongolian gazelle across years with the multiple-year movement data of multiple individuals, offering unique insights into understanding the space-use patterns of nomadic movements, which have direct conservation implications. I found pronounced individual variability in within and between year space use with especially high unpredictability in wintering and calving locations. This unpredictability in space use leads to estimates of individual lifetime ranges of 100,000 km². Importantly, the existing protected areas played only a minor role in the space use of Mongolian gazelle, with protected areas being too small to cover even the annual range of a single individual. I therefore advocate a landscape-level approach and highlight the importance of landscape permeability for the conservation of nomads.

For the third research objective, I used existing multi-species GPS movement data to quantify the variability in movement behaviors across four ungulate species (khulan, Mongolian gazelle, goitered gazelle *Gazella subgutturosa*, saiga antelope *Saiga tatarica mongolica*) in the Gobi-Steppe Ecosystem in Mongolia. I evaluated the differences in forage- and water-driven nomadic movements. I found that in the resource-rich mesic steppe in semi-arid landscape, which is characterized by spatially variable and temporally unpredictable foraging resources, animals undertake exceptionally long distance movements without frequently using any particular areas. In contrast, in resource-poor xeric desert, where broad-scale foraging resources are less variable, spatially predictable and temporally unpredictable watering areas serve as a main driver of nomadic movements, constraining movements and leading to frequently using certain areas.

These findings in my thesis highlight the importance of multiple-year monitoring data for characterizing nomadic movements and providing a useful road map to address the conservation challenges of nomadic ungulates. Nomadic ungulates cannot be conserved effectively in static protected areas; instead, their needs must be incorporated into conservation planning at the landscape scale which considers landscape permeability. Forage-driven nomadic animals, which have low recursion, permeability across the entire landscape must be the key concern. For water-driven nomadic animals, landscape permeability as well as the distribution of water bodies and their functional connectivity are main concerns for maintaining nomadic movements in arid landscapes.

2 INTRODUCTION

2.1 Movement ecology: From technologies to animal movement and conservation

Movements on land, in air, and in water are important traits of animals. They are key to find resources or mates and to escape enemies. Due to their major role in various ecological, behavioral, and evolutionary processes (Kays et al., 2015), animal movements have been studied extensively since the early days of scientific investigation. For example, bird banding was first used in 1890 by the Danish biologist Hans Christian C. Mortensen to study the movements of birds (Cleminson and Nebel, 2012). To gain more insight into organism movement, researchers and conservationists have employed various tracking technologies, including radar, acoustic and VHF telemetry, geolocators, and GPS receivers (Global Positioning System) (Cagnacci et al., 2010; Gibbons and Andrews, 2006; Harper, 1958; Rutz and Hays, 2009). Nowadays, GPS satellite tracking technology is utilized to study relatively fine-scale movement behaviors in free-ranging wild animals as well as movement processes at a global scale (Kays et al., 2015).

Due to technological advances that have revolutionized data collection on animal movements and environments, movement ecology has recently emerged as a research discipline which is concerned with animal movement, its causes, and its consequences across a wide range of taxonomic groups, communities, and ecosystems (Holyoak et al., 2008). In addition to technological advances, new conceptual frameworks have been developed in the past decades that better place animal movements and their *internal* and *external* drivers in ecological and behavioral contexts (Figure 1). For example, Nathan et al. (2008) introduced a unifying framework for movement ecology. The main component of this framework is the individual movement path, which is the outcome of the interaction between three internal and one external movement components: the *motion capacity*, the *navigation capacity*, the *internal state* of the individual, and the *external factors* affecting movement. Individual-level movement paths are produced by the interaction between these four components and represent elementary units that enables researchers to better understand three fundamental questions about animal movement: how the animal moves; when and where the animal moves; and why the animal moves.

In this framework, an individual's motion capacity is derived from a suite of traits that enables the individual to move, such as enabling butterflies to fly, fish to swim, large ungulates to walk and run, and spiders to balloon; hence, it addresses the question of how the animal moves (Dickinson et al., 2000). The navigation capacity is the suite of traits that enables the individual

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to orient its movement in space and time, corresponding to the question of where and when the animal moves. For instance, organisms return to previously visited areas by using the memory of previous experience (location and direction) and leave areas when they sense extreme environmental conditions (Bracis and Mueller, 2017). The internal state encompasses all factors specific to the focal individual that affects its propensity to move, addressing the questions of why the animal moves and what motivates this movement. It stems from evolutionary payoffs, such as juveniles leaving their natal group to breed or following adults to learn (Teitelbaum et al., 2016). The external factor combines all the biotic and abiotic environmental factors influencing the focal individual's movement. External factor should also include the human impact on the environment.

A different framework was introduced by Mueller and Fagan (2008) integrating individual-level movements with the patterns of resource dynamics, resulting in patterns of population-level movements. They summarized three movement patterns at the population level: range residency, migration, and nomadism. In landscapes where resources are sufficiently abundant year-round and their spatial distributions are less variable over time, animals remain sedentary – either with home ranges or territories. In contrast, landscapes where the spatial distribution of resource availability varies over time but the resource locations are predictable should support migration, whereas resource locations that are unpredictable over time should support nomadism.

Moreover, individuals' movements are also considered to be mobile linkers of resources, genetics, and processes between communities and ecosystems, which in turn can affect intra- and interspecific interactions, and thus modifying species' co-existence and biodiversity (Jeltsch et al., 2013). Mobile linkers interact with other species in a community and in environments in a specific area, and the outcomes of these interactions can maintain species' co-existence and biodiversity. Linking individual-level movement processes to biodiversity research can improve the understanding of biodiversity dynamics and provide insights for biodiversity conservation. Finally, Allen and Singh (2016) introduced a framework linking movement ecology with wildlife management and conservation. This framework highlights the importance of knowing the key movement pattern characteristics at the population level and their ecosystem impacts to determine the scale and type of conservation management needed as well as to make effective conservation decisions.

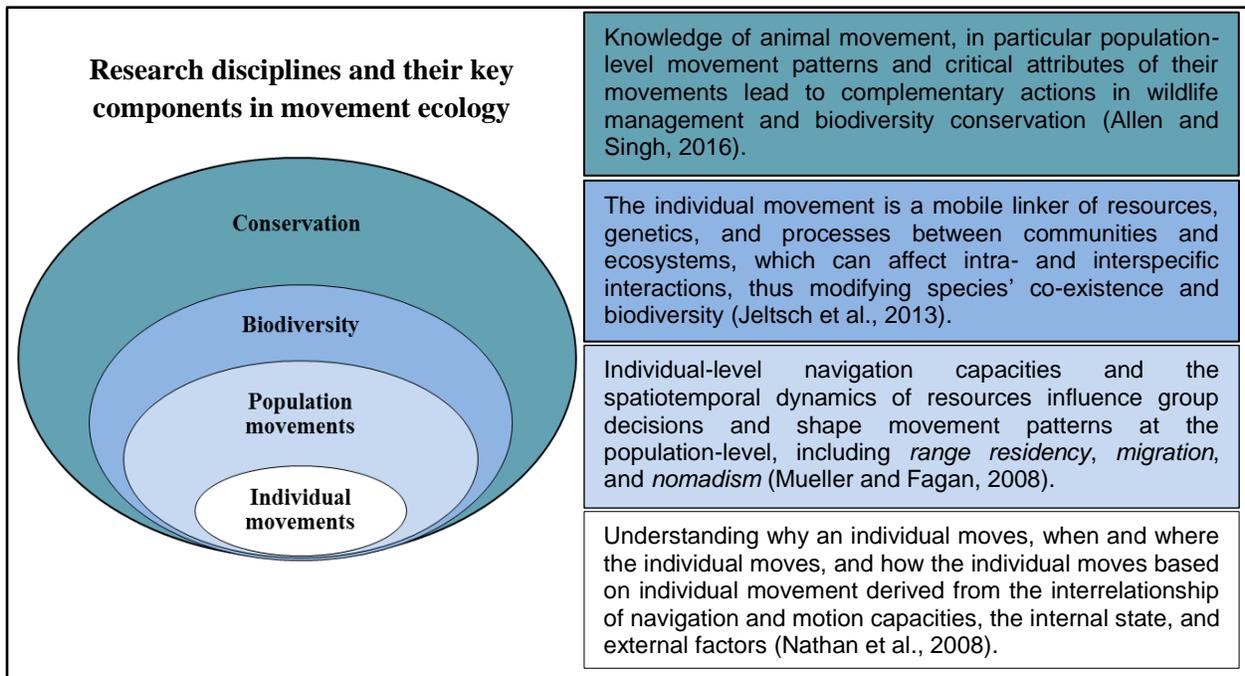


Figure 1. The linkage between conceptual frameworks in movement ecology: from the individual movement to population and biodiversity movements and conservation.

Conservationists have two main challenges in the attempt to increase the conservation impacts on highly mobile animals. One challenge is dealing with far ranging, landscape-scale movements and another challenge is dealing with animal movements with respect to dynamic environmental conditions in space and time. Overall, within the field of movement ecology, there is increasing recognition of the importance of the spatial and temporal dynamics on both fine- and broad-scale ecological processes. A key challenge is to understand the causes and consequences of movement to obtain an integrated understanding of animal movements and to plan conservation strategies accordingly.

2.2 Resource distributions and movement patterns

Environmental conditions (e.g., vegetation cover, precipitation, temperature) vary across space and over time, eventually determining whether an organism can occur in a particular location at a given time or whether the organism avoids the location. Specifically, the spatial and temporal changes of the resource distribution have been recognized as key drivers in determining the distribution and abundance of organisms, in particular, organisms foraging for resources, such as pollinators foraging for nectar or pollen, frugivorous foraging for fruits, and herbivores foraging for plants (Holdo et al., 2009; McIntyre and Wiens, 1999; Tucker et al., 2019).

Movements in response to the environmental conditions can be seen as a general strategy for dealing with such changes, with movements assuming a variety of forms across species and across spatial and temporal scales (Fryxell et al., 2008; Singh et al., 2012). To better understand and model animal movements, ecologists have classified the various movement types of animals into movement patterns, depending on the individual-level movement decisions and patterns in resource distribution. The movement patterns include three major population-level movements: range residency, migration, and nomadism (Mueller and Fagan, 2008).

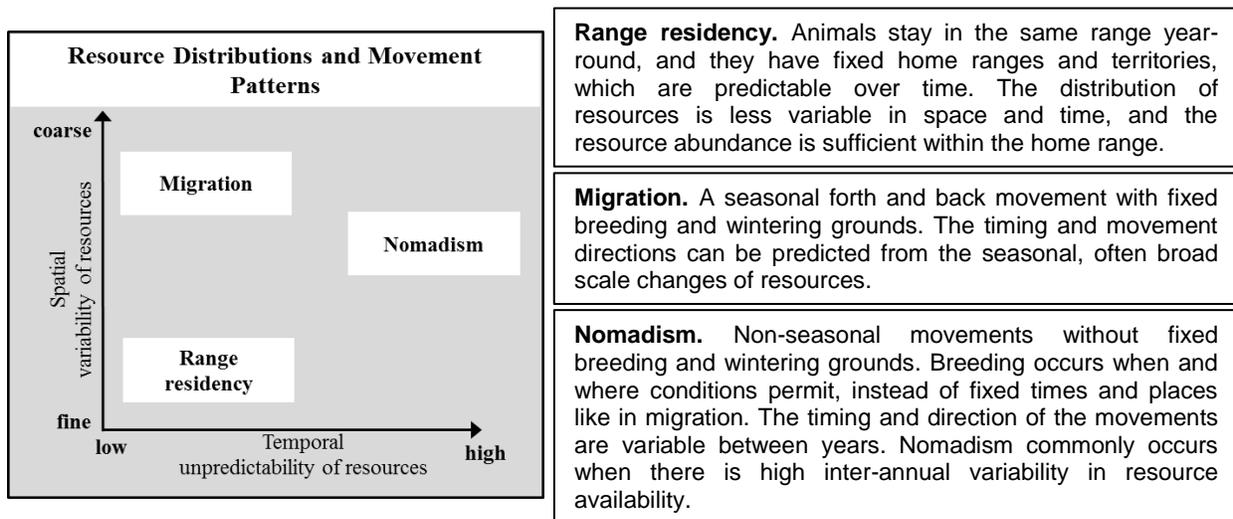


Figure 2. Variability of resource distribution and three major population-level movement patterns with their movement characteristics. The figure is adapted from Mueller and Fagan (2008), and the definitions of movement patterns are adapted from Runge et al., (2014).

Being resident on an annual range involves having stable home ranges or territories, where an individual occupies a relatively small area compared to the population distribution (Abrahms et al., 2017b; Mueller and Fagan, 2008). Migration is a seasonal, round-trip movement between spatially disjunct seasonal areas (Dingle and Drake, 2007; Joel, 2004). Nomadism differs from residency and migration because individuals do not engage in seasonal movement, and the annual movement differs from one year to another (Mueller and Fagan, 2008; Potts et al., 2016; Singh et al., 2012). One additional animal movement is dispersal, which includes natal and breeding dispersal occurring only once within an individual’s lifetime (Bunnefeld et al., 2011; Howard, 1960).

Although migration and nomadism both comprise long-distance animal movements driven by temporal variability in the distribution of resources, their main difference lies in the regularity of the movements, which in turn depends on the temporal predictability of the resources (Jonzén and Knudsen, 2011; Mueller and Fagan, 2008). It is important to distinguish

the difference between temporal variability and temporal predictability in the distribution of resources. If the locations of resource availability are seasonally distinct but the distribution patterns are the same in the following year, the resources would be temporally variable in a given year but predictable between years, favoring migration. In contrast, if the distribution of resource availability not only changes in a given year but the distribution pattern is different in the following year, resources would be temporally variable and unpredictable, favoring nomadism. In the following I first briefly review the well-studied migratory movements and after that provide a synopsis of the less studied nomadic movements.

2.3 Migratory movements

Animal migration can be driven by seasonally changing resource availability within a year, escape from predators, parasites, disease, competition, and harsh climatic conditions (Avgar et al., 2013, 2014; Dingle and Drake, 2007). Other drivers include factors related to social behavior, such as promoting juvenile survival and searching for mates and nesting sites (Avgar et al., 2014). While acknowledging the role of predator avoidance and competition as important for the evolution and maintenance of many migrants, in this thesis, I focus on changes in resource availability.

Migration occurs in various taxonomical groups, including birds, fishes, amphibians, reptiles, mollusca, arthropods, and mammals, and in highly seasonal climates around the planet, the individuals in these groups move to survive and reproduce (Dingle, 2006). Migrants follow ecological gradients in precipitation or temperature, often across elevations and/or latitudes (e.g., moving to different levels of a mountain or across a plain), to take advantage of seasonally variable resource availability (e.g., water or food availability) and escape inhospitable conditions (Fagan et al., 2013; Fryxell and Sinclair, 1988; Shaw and Couzin, 2013). In doing so, they find locations where the environmental conditions can improve the chances of survival and successful reproduction (Morales et al., 2010).

Among the various migrants, birds are well-studied, and many examples for migratory birds illustrate a remarkably diverse array of migratory behaviors (Hanson et al., 2015; Somveille et al., 2013; Viana et al., 2016). The classic bird migration is biannual migration, where the birds move between breeding and wintering grounds (Dingle, 2008). Birds track vegetation dynamics, and they move northward, timed with the seasonally increasing green-up of vegetation (Araújo et al., 2017). The breeding grounds are suitable habitat for nesting and for the survival of the

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hatchlings/fledglings, whereas the wintering grounds are more suitable for post-fledgling and adult survival. For example, the Arctic tern *Sterna paradisaea* migrates more than 70,000 km annually from the Arctic Greenland breeding grounds to the Southern Ocean for wintering grounds (Araújo et al., 2017). Birds use several different types of cues to navigate, and they can get compass information from the sun, the moon, the stars, and the earth's magnetic field (Able, 1993; Johansson et al., 2002; Muheim et al., 2018).

While a few species complete their long-distance migrations in one big push, most break up these long flights by resting and refueling at a specific area along the migration route (Buler et al., 2007; Hutto, 1998). Migratory birds need to use such sites frequently, so they can obtain small amounts of high-quality food to fuel their energy and continue their migration to reach their destination. These foraging patches are known as “stopovers”. Migratory birds repeat these long-distance movements every year, and thus the breeding and wintering grounds, stopover sites, and their migration routes can be predictable in space over longer periods. This tendency for animals to return to the same habitats year after year is termed “fidelity” (Switzer, 1993). Migratory birds exhibit fidelity to their migration corridors, seasonal ranges, and stopovers, and the timing of migration departures and arrivals (when to leave and arrive) and the direction of movement (where to go) can be predictable in space and time.

Among the migratory land mammals, ungulate species perform the most visible migrations (Fryxell and Sinclair, 1988). Migratory ungulates are native to every continent except for Australia and Antarctica, and they occur across Arctic tundra, Serengeti grasslands, and the Eurasian Steppe (Berger, 2004; Holdo et al., 2009; Sawyer et al., 2016; Singh et al., 2010a). In temperate latitudes with extreme seasonal variation in climate, ungulates follow elevational gradients (Berger et al., 2006; Sawyer et al., 2009). This is particularly true for montane ecosystems, where vegetation growth is strongly temperature-dependent (Pettorelli et al., 2005). Ungulates migrate from summer ranges, where they obtain high-quality forage or reduce competition and predation risk during calving time, to winter ranges with less snow cover or improved shelter from cold temperatures, snow, and wind (Hebblewhite et al., 2008; Nicholson et al., 2016; Singh et al., 2012). In the tropics, migratory ungulates usually follow rainfall gradients that trigger a flush of nutritious forage, migrating from the more arid habitats used during the brief growing season to higher rainfall areas used during the driest part of the year (Boone et al., 2006; Fryxell et al., 2004). In Arctic regions, for example, caribou, the northernmost ungulates, inhabit tundra and taiga habitats across Alaska, northern Canada, and Siberia (Bernes et al., 2015;

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Mallory and Boyce, 2017). Their migration follows latitudinal migration and some caribou live in low-snow areas and migrate only a few kilometers, while others travel hundreds of kilometers throughout the year to access high-quality forage and calving sites in the far north (Bernes et al., 2015; Mallory and Boyce, 2017). In the tropics, for example, the blue wildebeest completes the most famous and well-studied migration on earth. Up to 1.4 million wildebeest follow rainfall patterns between wet and dry season ranges that cover some 25,000 km² (Thirgood et al., 2004)

In addition, for herbivores, plant phenology is a key factor shaping their movements (Fryxell and Sinclair, 1988; Wilmshurst et al., 1999). Herbivores balance forage quality and quantity by consuming vegetation at intermediate biomass because net energy intake is mediated by a trade-off between intake rate and digestibility - called the forage maturation hypothesis (Fryxell, 1991). Because plant growth is delayed at high elevations and latitudes in spring, vegetation green-up moves as a resource wave along the elevational gradient across a large landscape. Detailed studies in ungulate migrations tested the green wave hypothesis (GWH), examining how ungulates track vegetation green-up in spring, where forage quality is highest. The GWH provides a conceptual framework for understanding how the movements of herbivores are timed to respond to resource waves. The studies examining the relationship between the movements of ungulates and the vegetation green-up wave showed that the migratory mule deer *Odocoileus hemionus* surf the green-up in spring along the migration routes in Wyoming, USA (Aikens et al., 2017), whereas the red deer *Cervus elaphus* jump the green-up wave, moving rapidly from winter range to summer range (Bischof et al., 2012).

Due to the distance between wintering and breeding grounds, migratory ungulates require vast, intact landscapes (Runge et al., 2014). In many parts of the world, development like intensive agriculture, urbanization, pipelines, railroads, roads, and fences has already cut up landscapes and blocked historic migrations (Kuile et al., 2018; Kunz et al., 2010; Wilcove and Wikelski, 2008). As these land use changes fragment more of the planet, wildlife migrations are increasingly threatened and numerous long-distance migrations perished across the globe before researchers even began to fully understand them (Tucker et al., 2018). Nevertheless, based on the fidelity to critical sites along the migration routes, conservationists protect migratory animals, focusing on preserving the critical habitats of wintering and breeding and/or summer grounds, stopover sites, as well as migration corridors (Abrahms et al., 2017a; Sawyer et al., 2012; Sawyer and Kauffman, 2011).

2.4 Nomadic movements

2.4.1 Characteristics of nomadic movements

As mentioned above, migratory animals move between seasonal ranges, which are often driven by predictable resource distributions along elevational gradients in space and time across years. The migrants' movements are characterized by coordinated movements among individuals and frequent return movements to previously visited areas, resulting in the repeated use of seasonal ranges, stopover sites, and movement corridors over long-term periods (Avgar et al., 2014; Bauer and Hoyer, 2014; Dingle, 2006). While nomadism is a long-distance movement behavior such as the one migrants display, it mainly differs in the unpredictability of timing and direction of movements across years (Dean, 2004; Mueller and Fagan, 2008; Roshier et al., 2008b). Nomadic animals move between favorable areas that are unpredictable in space and time and their movements are characterized by (i) uncoordinated movements among individuals, representing high individual variability (Jonzén and Knudsen, 2011; Mueller et al., 2011); (ii) infrequent return movements to previously visited areas, leading to lack of fidelity to seasonal ranges, movement corridors, and key areas including breeding and wintering grounds (Dean et al., 2009; Kingsford et al., 2010; Mueller et al., 2008; Runge et al., 2016); and (iii) aggregation in large numbers at a specific area followed by a possible absence for several years (Dean, 2004; Olson et al., 2009a). In brief, nomadic movement is a non-seasonal and irregular long-distance movement in which where and when to move as well as when and where to stop are unpredictable over time. Due to nomads' lack of fidelity to key areas and movement corridors, conserving nomadic species presents an extreme challenge and conservation strategies for them are rare (Allen and Singh, 2016; Runge et al., 2014). Although nomadism is not as well understood as migration, some studies have described nomadic movements by using a movement dataset combined with a long-term and large-scale survey database (Pedler et al., 2018, 2014).

2.4.2 Variability in nomadic movements

Nomadic animal movements are widespread and occur across a large range of different taxa, including amphibians, birds, carnivores, omnivores, marine animals, as well as large ungulates (Figure 3). There are different patterns of nomadic movements: some species move nomadically only at certain time of a single year, some individuals in the same population exhibit different movement patterns while others are nomadic throughout their lifetimes. For example,

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the movements of the cane toads *Bufo marinus* in Australia are restricted to areas with water that provide shelter, which results in the cane toads' strong fidelity to shelter sites in the dry season (Schwarzkopf and Alford, 2002). In contrast, in the wet season, when water availability is greater, they undertake nomadic movements with infrequent returns to previously used shelter sites.

This seasonal difference in movements suggests they are seasonally nomadic, with movements driven by seasonally changing suitable habitats and/or resources. An example of a species having different nomadic movement patterns are colonies of the forest tent caterpillar *Malacosoma disstria* in Canada, which have shown variability in their movements and fidelity to feeding sites, depending on the quality of the host plants where they forage (Plenzich and Despland, 2018). The colonies feeding on maples (low-quality forage) are nomadic, resulting in lower site fidelity to feeding sites and lower cohesion, while colonies feeding on aspens (high-quality forage) showed sedentary movement behavior.

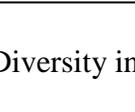
SPECIES	MOVEMENT DRIVERS	PATTERNS	REFERENCE
Forest tent caterpillar moth (<i>Malacosoma disstria</i>)  <small>© 2008 Will Cook</small>	Decreases in food quality. Caterpillar colonies feeding on maple, a poorer quality host plant showed higher mobility, low site fidelity to feeding sites, lower cohesion, and lower growth rate when compared those feeding on aspen.	Partially nomadic Caterpillar colonies feeding on poorer quality host plants are nomadic whereas those feeding on higher quality host plants are resident.	Plenzich and Despland, 2018
Cane toads (<i>Bufo marinus</i>)  <small>© Alamy stock</small>	Seasonally changing suitable habitats In the dry season, the movements of cane toads are restricted to areas with more water, resulting in fidelity to shelter sites. In contrast, in the wet season their movements become nomadic because shelter sites are more available, resulting in the lack of site fidelity.	Seasonally nomadic (Cane toads showed return movements to previously visited areas in dry season, but they had infrequent return movement in wet season).	Schwarzkopf and Alford, 2002
Caribbean spiny lobster (<i>Panulirus argus</i>)  <small>© San Diego reader</small>	Changes in foraging patches Spiny lobsters show nomadic movement when moving to better foraging areas. Female lobsters move to deeper water to release eggs and then return.	Fully nomadic Nomadic movements of Caribbean spiny lobsters are observed throughout a year	Bertelsen, 2013
Snowy owl (<i>Bubo scandiacus</i>)  <small>© Floyd Davidson</small>	Unpredictable distribution in prey abundance The snowy owls settle to breed in areas where high abundance of lemmings that is highly dynamic in space and time.	Fully nomadic Breeding and wintering sites of snowy owls are spatially variable across years.	Therrien et al., 2014 Robillard et al., 2016
Thomson's gazelle (<i>Eudorcas thomsonii</i>)  <small>© Yathin S Krishnappa</small>	Temporal changes in forage quality The spatial distribution of Thomson's gazelle is closely associated with the quality of forage, where great abundance of Thomson's gazelle are observed in patches with high quality vegetation.	Fully nomadic The distribution change in Thomson's gazelle was consistent throughout a year.	Fryxell et al., 2004
Grizzly bear (<i>Ursus arctos</i>)  <small>© Ronan Donovan</small>	Temporal changes in suitable habitat distribution It is hypothesized that temporal changes in food availability can be a driver of nomadic movement of the grizzly bear.	Fully nomadic Grizzly bears did not show fidelity to seasonal and also annual ranges between years.	Edwards et al., 2009
African lions (<i>Panthera leo</i>)  <small>© Maggy Meyer</small>	Competition for mates (prides) Some male lions are nomadic, where they are highly mobile passing through pride ranges. In contrast to resident males, nomadic males do not roar.	Partially nomadic While some male lions are resident other males are nomadic in the same population.	Grinnell and McComb, 2001

Figure 3. Diversity in nomadic movements.

This difference in the colonies' patterns indicates that they are partially nomadic, which is similar to partial migration, where some individuals in a single population are resident, others migrate within a single population, and individuals display consistent movement behaviors over time. The main difference is that nomadic individuals do not show strong fidelity to their movements across years. Some species are fully nomadic, moving long-distances over the course of a year, with movement patterns that do not occur in the following year. Some animals with fully nomadic movements are, for example, Thomson's gazelle *Eudorcas thomsonii* in the Serengeti (Fryxell et al., 2004) and grizzly bears *Ursus arctos* in Canada's Arctic, whose movements are driven by unpredictable changes in resource quality and quantity (Edwards et al., 2009).

2.4.3 Drivers of nomadic movements

Some recognized drivers of nomadic movements include (i) unpredictable spatiotemporal changes in resources; (ii) extreme climatic events, including droughts, severe winters, and flooding rains that result in resource pulses; and (iii) competition for suitable resources or mates.

The most commonly observed driver of nomadic movements is unpredictable changes in resources, leading to resource-driven nomadism (Dean, 2004; Roshier et al., 2008a). Nevertheless, the changes in resources can differ in their spatial and temporal predictability: resources can be spatially predictable but temporally unpredictable or resources can be both spatially and temporally unpredictable (Mueller and Fagan, 2008). For example, the presence of water at relatively predictable wetlands is an essential habitat resource for all waterfowl and other animals in desert ecosystems (Dean, 1997; Henry et al., 2015). Wetland resources are mostly temporary and non-seasonally available, but the locations of wetlands are relatively predictable. In contrast, patches with good forage (e.g., vegetation, fruits, seeds) can be both spatially and temporally unpredictable, promoting nomadic movements (Mueller et al., 2008; Webb et al., 2014). These are different aspects of predictability in environments, and their differences in temporal dynamics may lead to different types of nomadic movements. Nomadic animals are mostly observed in drylands in particularly resource-poor and wide-open ecosystems in arid and semi-arid regions (Dean, 2004). Arid regions are characterized by a lack of water and sparsely distributed vegetation, with shrubland, grassland, and barren grounds (Huang et al., 2016; Ragab and Prudhomme, 2002). The amount and the duration of precipitation is usually stochastic, resulting in highly variable and unpredictable resources in both space and time. In particular, deserts, semi-deserts, and grassland steppe are the most frequently cited examples of

environments where nomadism occurs, including South and East Africa, Central and East Asia, Mongolia, the Western United States, the east coast of South America, and a large portion of Australia (Dean, 2004). Resource availability in these ecosystems is typically affected by unpredictable and highly variable rainfall and/or snow coverage, but it is not yet clear whether there is an underlying common environmental factor for promoting nomadic behavior. However, all animals inhabiting these ecosystems have to adapt to unpredictable and fluctuating resources; the movement of nomadic animals is most often considered a response to environmental fluctuations and is typically driven by temporally unpredictable resources that are needed for survival and reproduction (Jonzén and Knudsen, 2011; Mueller et al., 2011; Roshier et al., 2008a). For example, many waterbirds occurring in arid regions of Africa and Australia are adapted to a temporally variable mosaic of ephemeral wetlands and their movements are driven by the dynamics of rainfall and primary productivity (Dean, 1997; Runge and Tulloch, 2016).

Another driver of nomadic movements is the escape of local conditions affected by extreme climatic events such as droughts and severe winters, when they occur. The dickcissel *Spiza Americana*, a small seed-eating bird, avoids areas with low productivity during droughts (Bateman et al., 2015), shifting their distribution range. Asiatic wild asses *Equus hemionus* move long distances to find new locations to survive during severe winter conditions (Kaczensky et al., 2011a). Though the most studies on nomadic movements focus on birds and identifying the different environmental drivers of their nomadic movements, little is known about nomadic movements driven by competition (Figure 3) (Grinnell and McComb, 2001; Plenzich and Despland, 2018).

2.4.4 Nomadic ungulates in the world

Although nomadic movements of several ungulate species around the world have been observed (Figure 4), they have not yet been studied to the same extent as nomadic movements of birds. A number of nomadic ungulates have been observed in arid and semi-arid regions of Africa. Gemsbok *Oryx gazella* inhabit arid, semi-arid bushland and grassland in Namibia and in adjacent South Africa, and they are viewed as nomadic (Furstenburg, 2016). Thomson's gazelle *Gazella thomsoni thomsoni* in the Serengeti exhibit nomadic movement, which is driven by changes in the spatial distribution of short grasses (Fryxell et al., 2004). Deserts in Saudi Arabia also have nomadic ungulates, including Arabian sand gazelle *Gazella marica* (Cunningham and Wronski, 2011) and Arabian oryx *Oryx leucoryx* (Tear et al., 1997), which are both considered

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nomadic ungulates. Moreover, the Sonoran pronghorn *Antilocapra americana sonoriensis*, an endemic species to western North America, is a nomadic ungulate in the Sonoran Desert, whose movements, according to researchers, are partly driven by the variability in forage quality and water availability (U.S. Fish and Wildlife Service, 2015).

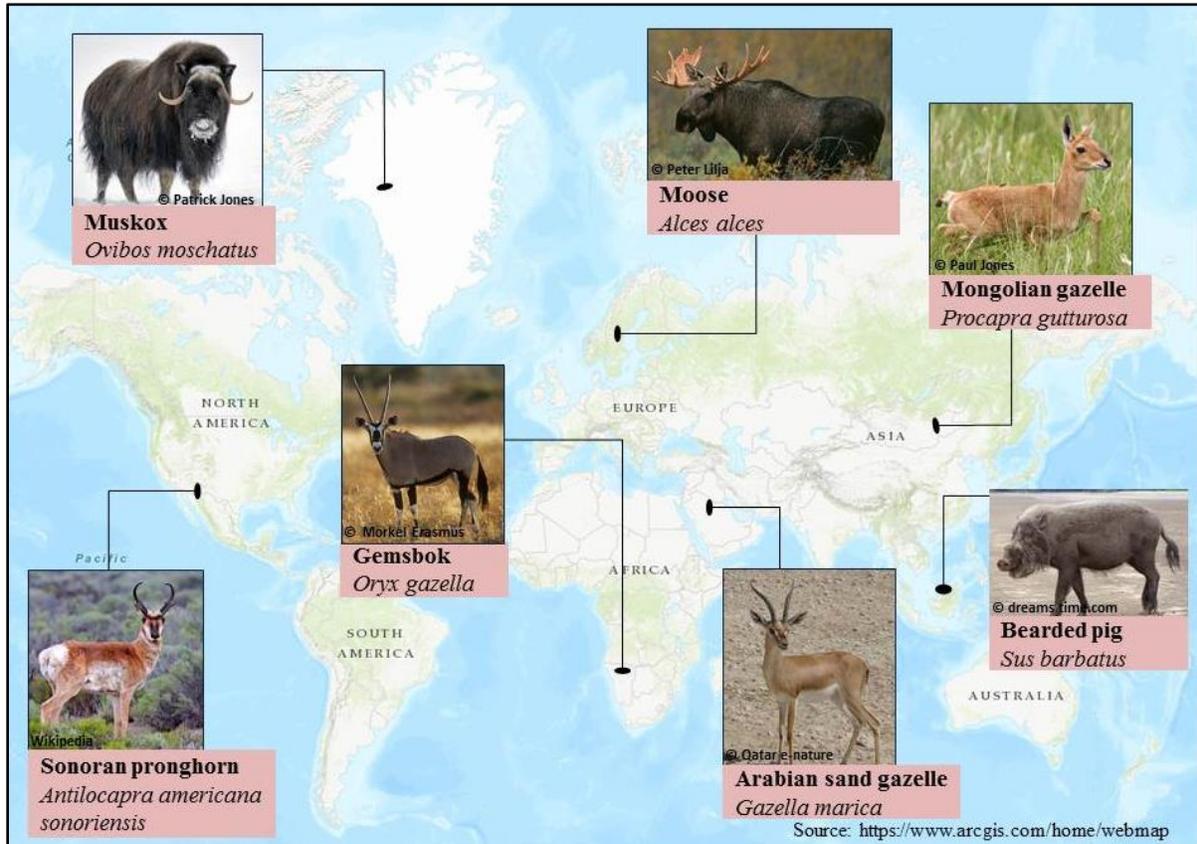


Figure 4. Nomadic ungulates around the world.

Sonoran pronghorn require large expanses of contiguous habitat to cope with the harsh environmental conditions in the desert. For the population of moose *Alces alces* across Sweden, researchers have found great individual-level variability in their movement patterns: migratory individuals occur in northern Sweden, whereas in southern Sweden, the movements of some individuals are seen as nomadic (Singh et al., 2012). Similarly, the muskox *Ovibos moschatus* in high-arctic Greenland shows large individual variation in annual movements, varying from dispersal to nomadic movements (Schmidt et al., 2016). On average, the annual movement distance of an individual muskox is 780 km, and musk oxen exhibit non-seasonal movements which are driven by their search for suitable foraging patches. A relatively large number of nomadic ungulates have been observed in the central Asian steppe landscapes, including

Mongolian gazelle *Procapra gutturosa*, khulan *Equus hemionus hemionus*, and saiga antelope *Saiga tatarica mongolica*, that all occur in Mongolia and that will be described in more detail in the study region and species section below. Overall, while researchers have observed that unpredictable changes in resources such as suitable foraging patches and water availability can be drivers of nomadic movements for ungulates in highly dynamic environments (Hancock et al., 2006; Mueller and Fagan, 2008), the drivers and patterns of nomadic ungulates are still poorly understood and require further study. Furthermore, more research is needed on developing suitable conservation strategies for nomadic ungulates.

3 RESEARCH QUESTIONS

The overarching aim of my doctoral research is to examine and quantify the spatial variability in the movements of nomadic ungulates in Mongolia as well as examine the particular conservation challenges associated with nomadic movements. In this thesis, I focused on quantifying the key characteristics of nomadic movements to investigate three main areas of interest (Figure 5).

The first area of interest is determining the underlying environmental drivers of nomadic movements (Q1 in Figure 5), which I address by formulating the first research question: “Do the spatiotemporal dynamics of suitable habitat promote the high mobility of nomadic ungulates?” The second area of interest is identifying and quantifying the patterns of nomadic movement (Q2 in Figure 5), which leads to the second research question: “How variable is space use among individuals in the same year and between years? How predictable is space use between years?”. Here I am especially interested in understanding the between-year variability in space use and the related conservation challenges. Finally, the third area of interest is comparing the variability in nomadic movements across ungulate species and across environments (Q3 in Figure 5), which is addressed by the third research question: “How does nomadic movement behavior vary across ungulate species and their environments?”. In addition, based on the main findings from the three research questions, I frame key conservation measures for nomadic species that should be considered in conservation strategies. I address each of the three research questions through empirical case studies involving nomadic ungulates in Mongolia. Each research question corresponds to a research article that has been published by and/or submitted to peer-reviewed scientific journals. These research articles are included in the appendix (appendices A.1, A.2, and

A.3), and they provide details about the studies corresponding to the research questions below, including the methodologies, interpretation of the main findings, and supplementary materials.

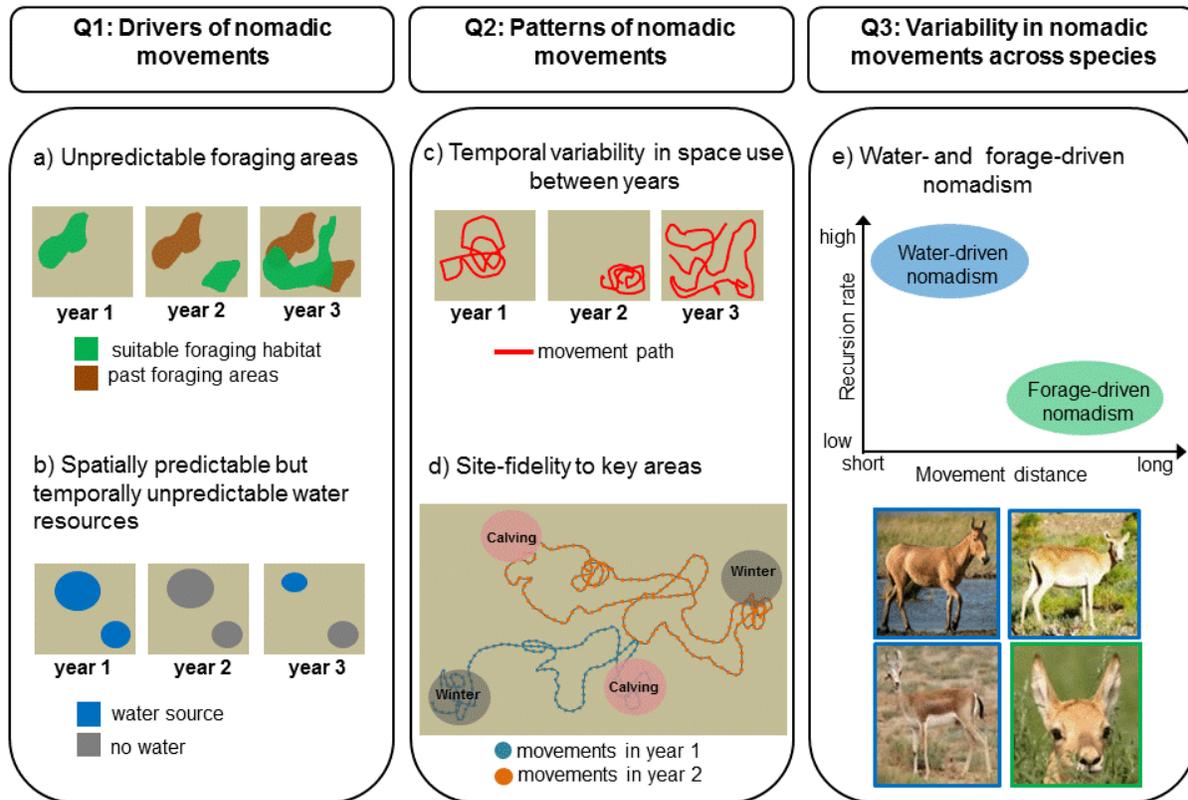


Figure 5. Conceptual framework quantifying the drivers (Q1) and patterns (Q2) of nomadic ungulate movements as well as the variability in nomadic movements across species (Q3). For Q1, I focused on two different types of drivers of nomadic movements: (a) both spatially and temporally unpredictable foraging areas and (b) spatially predictable but temporally unpredictable water resources. For Q2, I examined (c) the degree of temporal variability in the space use and (d) the site fidelity to key areas, including wintering and calving grounds. For Q3, I quantified (e) the water- and forage-driven nomadic movement behavior across four ungulate species (clockwise from upper left: khulan, saiga antelope, Mongolian gazelle, goitered gazelle), based on a variety of movement metrics.

3.1 Do the spatiotemporal dynamics of suitable habitat promote the high mobility of nomadic ungulates?

In arid and semi-arid regions where rainfall and snow coverage are variable in space and time, the availability of suitable resources tends to be unpredictable within a given season as well as between years (Jonzén and Knudsen, 2011). In such dynamic environments, nomadism is a strategy where animals respond to unpredictable changes in resource distributions. While the same-year variability and between-year variability in resources are known as possible drivers of long-distance nomadic movements, drivers of nomadic movements remain poorly understood

and little research has been done across ungulate species and ecosystems. I tested the underlying drivers for nomadic movements through a case study of the Asiatic wild ass (khulan in Mongolian), an equid species in Mongolia's Gobi Desert (Q1 in Figure 5). Specifically, I used long-term ground survey data on khulans and satellite remote sensing data on vegetation. I expected that the between-year spatially unpredictable nature of the khulan foraging habitat in the desert would promote the high mobility of khulan (for more details, see the Methods section in the thesis and Appendix A.1).

3.2 How variable is space use among nomadic individuals in the same year and between years? How predictable is space use between years?

The key conservation challenges for highly mobile species are their large ranges and the variability in their space use between years (Allen and Singh, 2016; Runge et al., 2014). Nomadic movements are characterized by non-seasonal spatial variability and a lack of temporal predictability in space use, un-coordinated movements among individuals, and a requirement for vast, intact landscapes, posing a significant conservation challenge. However, these key characteristics of nomadic animal movements, in particular for nomadic ungulates, and the potential implications for the animals' conservation, remain understudied, in large part due to a lack of suitable datasets for multiple individuals monitored across years. Furthermore, studies on the use of spatially fixed protected areas (PAs) or the effects of anthropogenic disturbance on nomadic ungulates are scarce. In addition to examining the spatiotemporal variability in space, I assessed current conservation measures and made future conservation recommendations through a case study involving Mongolian gazelle. I investigated the individual variability in the space use of Mongolian gazelle in the same year and between years using a multi-year GPS movement dataset (Q2 in Figure 5). Specifically, I was interested in the predictability of the space use between years and the individual variability in the estimated lifetime ranges as well as the implications for potential conservation measures. In addition, I examined the use of protected areas and the effects of anthropogenic disturbance on gazelle movements. Due to an emerging development in the Mongolian gazelle habitat, I assessed the effects of existing linear barriers on gazelle movements, and finally, I recommended specific conservation measures.

3.3 How does nomadic movement behavior vary across ungulate species and their environments?

The drivers of nomadic movement behavior vary across species and include spatiotemporal changes in ephemeral resource distribution (Bennetts and Kitchens, 2000), extreme weather events (Kaczensky et al., 2011a), and competition (Grinnell and McComb, 2001), which could lead to different types of nomadism. With regard to resources as drivers it is important to recognize that the ephemeral resources can be spatially predictable (e.g., water resources) or spatially unpredictable (e.g., high-quality patches with foraging resources) while temporally variable in their presence. This important difference in the resource distribution could trigger different types of nomadic behavior across species and ecosystems. I focused on examining the variability of movement behaviors across four ungulate species which could exhibit differences in forage- and water-related nomadism across the Gobi Desert and steppe ecosystems in Mongolia. I expected that in the xeric desert ecosystem, animals will show “water-dependent nomadism”, which could be driven by the temporal dynamics of spatially fixed water resources (Q3 in Figure 5). In water-dependent nomadism, animal movements are expected to be constrained by water sources, with animals frequently revisiting previously visited areas in a relatively short time. In contrast, in the mesic steppe, I expected that animals will show “forage-dependent nomadism”, with exceptionally long-distance movements and infrequent revisits to previously visited areas because spatially und temporally variable foraging resources are expected to be a main driver for movements.

4 STUDY REGION AND STUDY SPECIES

4.1 A nomadic landscape: The Gobi-Steppe Ecosystem

Mongolia is bordering China in the south and Russia in the north. It has a cold, semi-arid, extreme continental climate, with great seasonal changes, ranging from short, hot summers to long, cold winters. Because Mongolia’s rangeland is a non-equilibrium ecosystem (Fernandez-Gimenez and Allen-Diaz, 1999) in which the temperature and the amount and durations of precipitation are highly variable across seasons and years, there is spatial and temporal variation in the availability of vegetation (Vandandorj et al., 2015) and water sources.

I conducted my study in Mongolia’s Gobi-Steppe Ecosystem (GSE), covering an area of over 800,000 km² (Batsaikhan et al., 2014). The habitat types in the GSE consist of various

habitat types, ranging from herbaceous mesic steppe, covering eastern Mongolia (Eastern Steppe hereafter), to shrubby xeric Gobi deserts, covering south and southwestern Mongolia (Gobi Desert hereafter) (Figure 6) (Chimed-Ochir et al., 2010). The average elevation in the Eastern Steppe is 1000 m to 1300 m, increasing toward 1800 m in the southern Gobi Desert, whereas the southwestern Gobi Desert is surrounded by the high Altai Mountains, with elevations up to 4000 m (Buuveibaatar et al., 2013; Imai et al., 2017; Kaczensky et al., 2011b).

The Eastern Steppe is one of the largest temperate grasslands (Carbutt et al., 2017), with a cold steppe climate and an average annual precipitation of 300 mm (Centre and Wetterdienst, 2006). Its plant communities are predominantly herbaceous, with a mix of short grasses, sedges, and forbs, such as *Stipa krylovii*, *Stipa grandis*, *Carex duriuscula*, and *Cleistogenes spp*, growing on the flat plains. There are few perennial rivers in the steppe, and most places lack permanent surface water. To meet their water needs, wildlife rely on high-quality green vegetation during summer periods.

The Gobi Desert is characterized by a cold desert climate and is drier than the steppe, with an annual precipitation ranging from 50 mm to 200 mm (Kaczensky et al., 2011b). This is an open shrubland, where vegetation is sparse, with barren grounds and plant communities that are dominated by xerophytic shrubs and herbs as well as perennial forbs. Intermittent springs and ephemeral channels are sparsely distributed; in some places, there are oases, ephemeral dry river beds, and drainages. Water resources are particularly important for both humans and wildlife.

In contrast to the central part of Mongolia, the GSE is less populated by people. Nomadic herders with livestock inhabit the GSE, sustaining a great variety of wildlife, including steppe ungulates, such as Mongolian gazelle, goitered gazelle, saiga antelope, and khulan; mountain ungulates, such as Argali sheep and mountain goats; and carnivores, such as gray wolves, Gobi bears, snow leopards, and Eurasian lynx (Chimed-Ochir et al., 2010). Ungulate species, in particular, the steppe ungulates that I studied here, move long distances as part of a nomadic movement strategy, which sustains abundant ungulate populations by allowing them access to the best resources throughout time (Batsaikhan et al., 2014). The Gobi-Steppe Ecosystem is one of few regions where the nomadic movements of multiple ungulate species can be explored in the same region.

STUDY REGION AND STUDY SPECIES

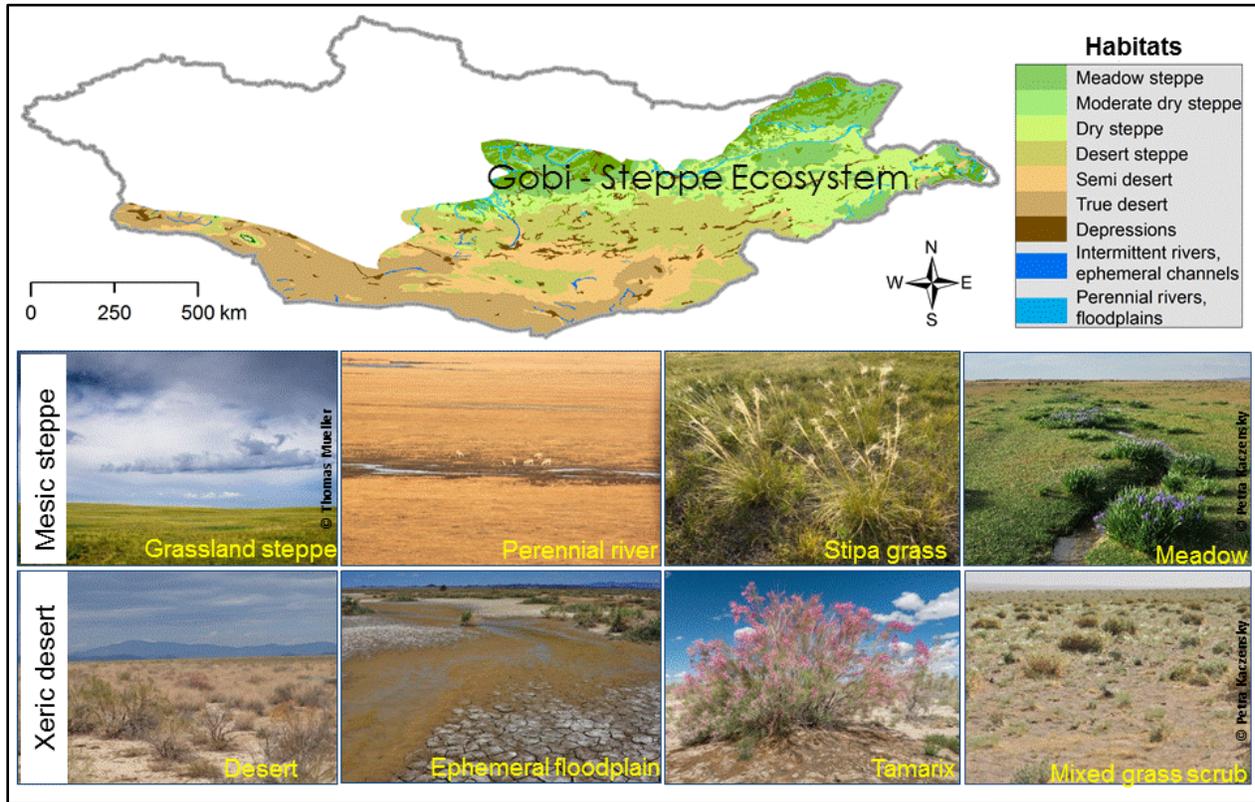


Figure 6. The distribution of the habitat types across the GSE. The map of the habitat types in the GSE is adapted from Chimed-Ochir et al. (2010).

4.2 Ungulate species in the Gobi-Steppe Ecosystem

Mongolian gazelle

The Mongolian gazelle is a medium-sized antelope (~ 30 kg) species that is native to the open steppe in Mongolia as well as the adjacent areas of Russia and China (Mallon, 2008). Population estimates vary widely depending on the survey methodology and intensity, and there are population fluctuations caused by disease and extreme conditions, such as droughts and severe winter conditions (Clark et al., 2006). In 2002, the population was estimated to be about one million. Remarkably, more than half of the world's Mongolian gazelle reside on the Eastern Steppe in Mongolia. In the International Union for Conservation of Nature (IUCN) red list, the Mongolian gazelle are listed as a least-concern (LC) species (Mallon, 2008), and the regional conservation status is endangered (EN) (Clark et al., 2006). Mongolian gazelle thrive among the open steppe and rolling foothills of the surrounding ranges, where they move long distances to find patches with high-quality forage.

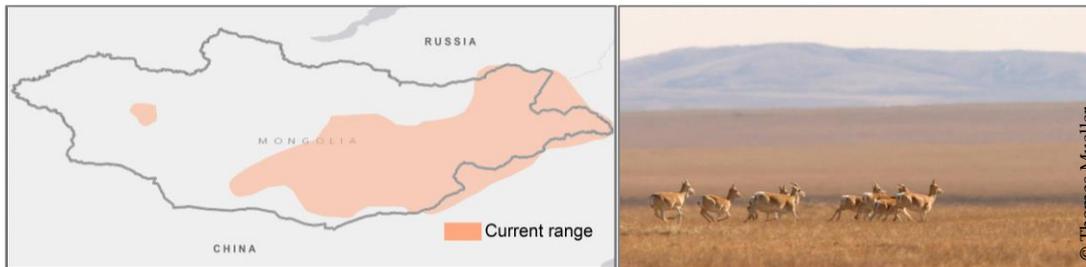


Figure 7. The global distribution of Mongolian gazelle. The map was made by the author based on the distribution range data from Mallon (2008).

Mongolian gazelle congregate in high-quality resource areas during summers with droughts (Olson et al., 2009a), and they undertake exceptional long-distance movements to escape severe winter storms. While the annual range of an individual gazelle covers an area of 32,000 km² (Olson et al., 2010), the estimated population range of the species in the Eastern steppe is 200,000 km² ± 3,100 km² (Fleming et al., 2015). The calving period starts in June and rutting season starts in early winter.

Goitered gazelle

The goitered gazelle is a medium-sized antelope (~30 kg) species. The distribution range of goitered gazelle covers Central Asia (Kazakhstan, Turkmenistan, Uzbekistan, and marginally Tajikistan and Kyrgyzstan), Iran, Afghanistan, Pakistan, northwest China, and Mongolia (IUCN SSC Antelope Specialist Group, 2017). Goitered gazelle inhabit a wide range of semi-desert and desert habitats, and according to the IUCN, the population has decreased. The current estimated population at global population size ranges from 42,000 to 49,000 individuals (IUCN SSC Antelope Specialist Group, 2017). In total, the recent population estimation of goitered gazelle in Mongolia is 5,900 individuals in the Dzungarian Gobi and 28,462 individuals in the southern Gobi, indicating that Mongolia's Gobi Desert contains more than 50% of the global population of goitered gazelle (Buuveibaatar et al., 2016b; Ransom et al., 2012). Therefore, Mongolia's Gobi Desert is a globally significant ecosystem in preserving the species. Little research has been done on the movement of goitered gazelle.

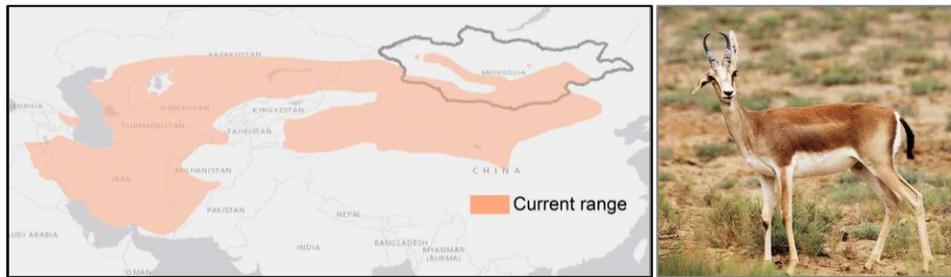


Figure 8. The global distribution of Goitered gazelle. The distribution range data is adapted from IUCN SSC Antelope Specialist Group (2017).

Saiga antelope

The saiga antelope is a medium-sized antelope (~35 kg) species that occurs across Russia and Central Asia's semi-arid rangelands in Kazakhstan, Uzbekistan, and Western Mongolia (IUCN SSC Antelope Specialist Group, 2018). Globally, their population numbers dropped from over a million in the early 1990s to around 165,000 individuals, due to unregulated poaching for horns and meat, extreme climatic conditions of droughts in summer, severe winters, and mostly due to a bacterial disease outbreak (haemorrhagic septicaemia) in 2015. The IUCN classifies saiga antelope as critically endangered (CR).



Figure 9. The global distribution of Saiga antelope. The distribution range data is adapted from IUCN SSC Antelope Specialist Group (2018).

There are two subspecies: *Saiga tatarica tatarica* and *Saiga tatarica mongolica*. The Mongolian Gobi Desert maintains a small population of Mongolian saiga, *Saiga tatarica mongolica*, an endemic species, and their population is estimated at 5,000 individuals in Mongolia (IUCN SSC Antelope Specialist Group, 2018). The Mongolian saiga occurs in semi-desert and dry steppe depressions in western Mongolia. The home ranges of individual Mongolian saiga range from 3,000 to 4,000 km².

Asiatic wild ass (referred to as khulan)

The khulan is one of seven wild equid species, with a body mass of ~250 kg. The estimated global population of khulan is 55,000 individuals, and their IUCN global status is near threatened (NT) (Kaczensky et al., 2015b). Small isolated populations occur in protected areas in India, Turkmenistan, Iran, and China. With an estimated 42,000 individual khulan, the southern Gobi Desert in Mongolia is a critical habitat for the largest remaining population of khulan (Buuveibaatar et al., 2016b). Khulan are predominantly grazers and hindgut fermenters.



Figure 10. The global distribution of khulan. The distribution range data is adapted from Kaczensky et al. (2015b).

They rely on a higher intake rate and forage abundance than ruminants in order to meet their nutrient requirements and maximize energy. Khulan are well adapted to coping with unpredictable resource distributions, covering long distances in search of water and pasture. Their annual ranges vary between 7,000 km² to 70,000 km² (Kaczensky et al., 2006), and GPS tracking data show that they move to new areas to escape areas affected by severe winter storms (Kaczensky et al., 2011a). Khulan are dependent on water sources in summer seasons (Kaczensky et al., 2010). Thus, the distribution of water sources probably strongly influences the khulan's distribution, space use, and movement patterns.

4.3 Barriers to the movements of ungulate species

On the move, the ungulates in this study encounter a number of threats, including poaching, competition with livestock for pasture, and foot-and-mouth disease (Bolortsetseg et al., 2012; Buuveibaatar et al., 2016a; Olson et al., 2011). In addition, linear barriers, such as fences along the Trans-Mongolian Railway and the Mongolian-Chinese and Mongolian-Russian borders, are a major risk factor in habitat fragmentation and habitat loss (Ito et al., 2008; Linnell et al., 2016; Olson et al., 2009b).

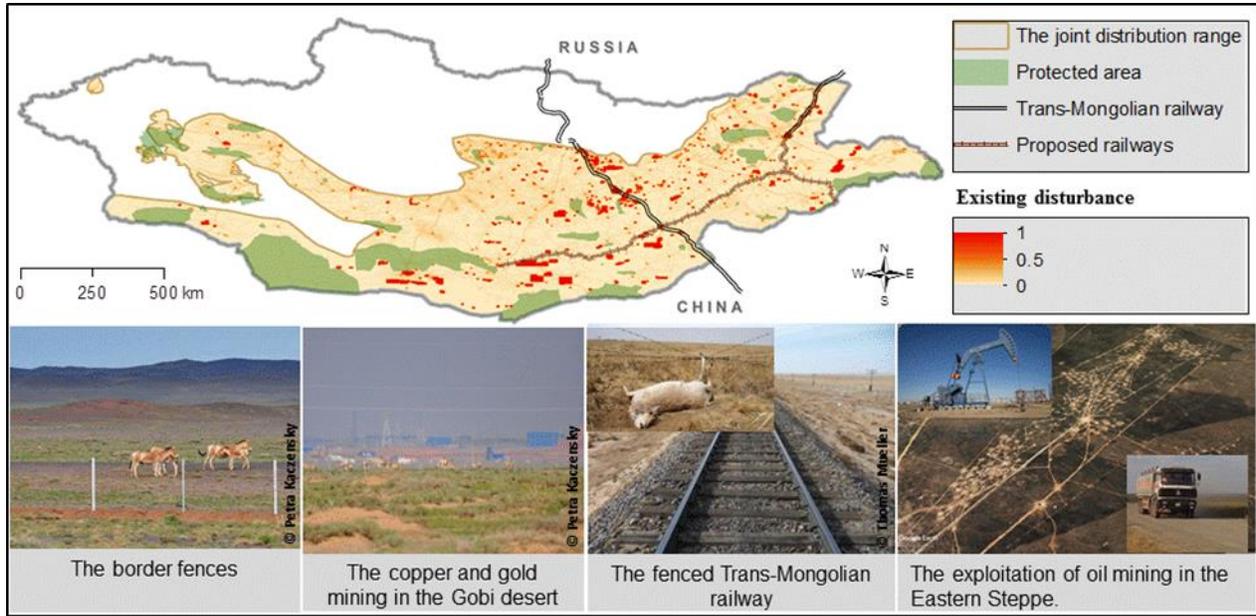


Figure 11. The existing and proposed disturbances across the joint distribution range of the four ungulate species in the GSE. The background image on the map represents a cumulative disturbance index layer (Heiner et al., 2016) including five human-induced factors: herder household locations, agricultural use, existing mining areas, population centers, and linear infrastructure, such road and railways. The disturbance index ranges from 0 (no disturbance) to 1 (high disturbance). The protected areas (green polygons) across the joint distribution range are not fenced. The national border and railway fences are, in fact, barriers for the movements of Mongolian gazelle, goitered gazelle, and khulan, but it is unclear whether newly emerging anthropogenic disturbances in the steppes also act as barriers and whether they could impede the connectivity among the protected areas. Detailed studies of these animals could provide a roadmap for future conservation efforts.

5 DATA COLLECTION AND RESEARCH METHODS

Long-term monitoring datasets are essential in quantifying the spatiotemporal dynamics of nomadic movements. In my investigation of the variability in nomadic ungulate movements in Mongolia, I used three different datasets. Two are multiple-year monitoring datasets that comprise ground-based census data as well as data collected by GPS tracking. The third dataset is a single-year dataset that included data across multiple species. For the first research question, which concerns determining the spatiotemporal variability in foraging habitats, I used a long-term ground-based line transect wildlife dataset that includes data on khulan, compiled by researchers and rangers associated with the Great Gobi Strictly Protected Area in Mongolia (Kaczensky et al., 2015a). For the second research question, I conducted field work myself in the Eastern Steppe in Mongolia, where I deployed GPS collars on Mongolian gazelle and collected a multiple-year GPS movement dataset to examine their space use and the resulting conservation implications.

For the third research question, I collaborated with researchers who shared their movement data on nomadic ungulates (which are listed as co-authors in the manuscript in appendix A.3). I used these multi-species GPS movement data to quantify the variability in movement behaviors across four ungulate species in the GSE. This section provides an overview of the methods that I utilized in the three studies. For more detailed information, especially regarding analysis and statistical methods, please see the Methods section for the particular study in appendices A.1, A.2, and A.3.

5.1 Drivers of nomadism: Measuring spatiotemporal dynamics in foraging habitat

For the first research question, which concerns drivers of nomadism and determining the spatiotemporal variability in foraging habitats, I used a long-term ground-based line transect wildlife dataset that includes data on khulan, compiled by researchers and rangers associated with the Great Gobi Strictly Protected Area in Mongolia. The dataset includes 33 surveys conducted to monitor the distribution and abundance of khulan and goitered gazelle, completed on a monthly basis between 2003 and 2010 (Kaczensky et al., 2015a). These ground-based surveys followed a distance sampling approach (Thomas et al., 2010), covering the entire study area (9000 km²). When the survey team detected khulan and goitered gazelle, they recorded the species name and group size and used the GPS coordinates and compass bearing to record their own location, their distance to the animals, and the sighting angle.

I aimed to model suitable khulan foraging habitat across time to investigate whether the foraging habitat is spatially variable and temporally unpredictable. As a basis for this model, I selected 12 surveys conducted between 2004 and 2009, covering the vegetation period from June until September. In total, the 12 surveys included 22,894 individual khulan recorded in 723 groups and 5387 individual goitered gazelle in 1136 groups. To construct a habitat model that characterizes the foraging habitat of khulan over time, I followed three main steps (for more details, please see appendix A1). First, I used the geosphere library in R to calculate the locations of the detected khulan based on the location of the survey team and the distances between the team and animals (Robert et al., 2016) and whether khulan are present or absent in a given 5 km² moving block along the transect line (Figure 1 in A.1). Second, I measured the relevant static and dynamic environmental variables in each block. The static variables include the distance to water, elevation, and the slope (°), as determined from a digital elevation model (DEM). I used the normalized difference vegetation index (NDVI) based on readings from NASA's Moderate-

Resolution Imaging Spectroradiometer (MODIS) as a dynamic environmental variable that can measure changes in vegetation greenness. I compiled 72 MODIS NDVI 16-day composites in total, representing the summer vegetation periods between 2004 and 2009. I then averaged values from each of above variables for each survey block in a given composite. Lastly, I built a dynamic habitat model for khulan based on combining the presence-absence data of khulan from the surveys with the environmental variables. In addition to the environmental variables, I include the presence-absence data of goitered gazelle to test for potential interaction effects with the presence of khulan. I also included protection zones in the protected area to test for effects of the protection status on khulan presence. For model validation, I use independent GPS movement data of khulan in the Dzungarian Gobi (Figure 2 in A.1).

5.2 Patterns of nomadism: measuring space use over time

Over the last several decades, advances in wildlife tracking technology, including radio telemetry and GPS satellite collars, have enabled much richer data collections on animal movements. To quantify the individual-level variability in the space use of nomadic Mongolian gazelle, I collected multiple-year GPS tracking data for several individual gazelle. Together with a team of colleagues and supervisors, I conducted two field seasons in Mongolia’s Eastern Steppe, and I deployed GPS satellite collars on a total of 34 Mongolian gazelle.



Figure 12. The data collection process for tracking animal movements from catching animals, receiving GPS movement data to data analyses.

In October 2014, I fitted GPS collars on 15 individuals at a single location on the same day and in September 2015, on 19 individuals in the course of two weeks at four different locations. All

animals were captured following standard protocols approved by the Ministry of Environment and Green Development in Mongolia (A.2). I employed local people as field assistants, and the capture team consisted of 15 to 20 people, including drivers, assistants handling captured animals, and supervisors.



Figure 13. The GPS satellite collars that were fit on adult Mongolina gazelle record their movement positions in the Mongolian Eastern Steppe. (A) The LifeCycle collar (330 g) transmits one GPS position every 23 hours. (B) The solar-assisted LiteTrack GPS (350 g) transmits one position every hour. (C) GPS movement dataset from these GPS collars.

I caught Mongolian gazelle using nets, which is the most common capture technique for steppe ungulates in Mongolia. With the help of field assistants and drivers that I supervised (~15 people), I searched for gazelle while driving through the steppe. Whenever a group of gazelle was spotted, the assistants and I built nets close by (Figure 12). We then guided the group with four cars towards the nets over a maximum distance of 4 km. I then removed the entangled individuals from the nets. I used a blindfold to calm the animals and hobbles to restrain their legs to prevent injuries (Figure 12). I fit a GPS collar on each individual, took a hair sample, recorded the collar's identification numbers, the capture location, date, time, and sex and then released the animal from where it was netted (Figure 12). I used two different types of GPS collars. Based on my intention to monitor nomadic movements over multiple years, I chose LifeCycle 330 GPS collars for 28 individuals, which transmit 1 GPS position approximately every 23 hours and batteries that last up to 4 years (Figure 13A). In addition, I tested 6 solar-assisted LiteTrack GPS Iridium collars, which transmit one position every hour (Figure 13B). GPS collars record an animal's precise location with an associated date and time. The collars transmitted the dataset for the tagged individuals in real time, sending each data point to a satellite web services (Figure 13C).

I used this dataset to tease out the variability and predictability of the Mongolian gazelle's space used across years. I selected individuals that were monitored for at least 1 year and up to 3 years, yielding 22 individuals (19 females and 3 males). Because data was collected at two different time scales (23-hour vs. hourly GPS positions), I standardized the analysis, sampling the hourly location data from the collars into 23- and 24-hour intervals using the "SyncMove" R library (Rimmler and Mueller, 2015). For the analyses in this study, I used 12,166 daily GPS positions from 22 individuals that were monitored from one to three years (Figure 1 in A.2). Based on this dataset, I examined the variability of Mongolian gazelle's space use among individuals in a given year and across years for a given individual. I calculated the range size for each individual in each year, using a minimum convex polygon (95% MCP) as a metric of annual space use. In addition, I also calculated the estimated lifetime ranges per individual, using autocorrelated kernel density estimation (AKDE), a novel method that allows the use of autocorrelated GPS movement data (Fleming et al., 2015). I then compared the annual range size among individuals in a given year and between years to characterize the spatiotemporal variability of space use at the individual level. I also compared the lifetime space use among individuals to characterize the variability of the estimated lifetime ranges. Second, I examined the predictability of space use, quantifying variation in gazelle's space use during calving and wintering periods between years. For each individual female gazelle, I first divided two consecutive years into 14-day intervals, calculated the mean location of the gazelle for each interval, and then calculated the pairwise distances between the mean locations of the corresponding 14-day intervals between the years. The lower the pairwise distance value, the closer the gazelle is to its location during the same time (the same 14-day interval) the previous year. Third, I assessed the gazelle's use of protected areas and the effects of anthropogenic space disturbance (e.g., population centers or oil fields) on the space use of Mongolian gazelle (Figure 1 in A.2). Fourth, I also considered the effects of the Mongolian border fence on Mongolian gazelle movements. For each individual, I measure the travel distances along the border fence when the individual encounters the border. To assess the predictability of space use across years, the gazelle's use of protected areas, as well as the effects of anthropogenic disturbance on gazelle space use, I used randomly simulated movement paths as a null model. Further details on the methods, simulation model, and statistical analyses are provided in the method section and supplementary materials in appendix A.2.

5.3 Variability in nomadic movement behaviors

To examine the variability in the nomadic movement behaviors of ungulate species in the GSE, I collaborated with researchers who have previously collected GPS movement data for ungulates in Mongolia, namely, the researchers who coauthored the manuscript in appendix A3. Consequently, I compiled GPS movement data for the following species: Mongolian gazelle, goitered gazelle, saiga antelope, and khulan (Figure 1 in A.3). To supplement the movement data that I compiled, I added the GPS movement data that I collected myself of five Mongolian gazelle individuals.

These four species occur across the various habitats of the GSE and represent an array of taxa. The recording time interval of the GPS positions across species ranged from 15 min for khulan and up to 4 h for Mongolian gazelle. The tracking periods varied across species and ranged from 2006 periods for saiga antelope to 2017 periods for Mongolian gazelle. To achieve consistent fix rates for comparison, all the data were resampled to 4-h fix intervals, with the exception of the three saiga antelope individuals that were sampled at 5-h intervals. Given my research question regarding forage- and water-related nomadic movements, I focused on the months from April to October, when animals rely on green vegetation and water sources. I eliminated the winter months from November to March, when animals use snow to meet their water needs. Nevertheless, for this study, I only used a four-month movement dataset between April and July because some of the individual saiga antelope and khulan lack movement data from August to October. The final dataset resulted in 27,368 GPS positions of 40 individuals across the four species. The number of GPS positions for each individual ranged between 539 and 732 across the four months. The number of individuals for each species varied: 11, 6, 8, and 15 individuals for Mongolian gazelle, goitered gazelle, saiga antelope, and khulan, respectively.

To evaluate the variability of movement behaviors, based on this dataset, I followed three steps. First, for each individual, I calculated five movement metrics that are widely applied in current studies in movement ecology (Abrahms et al., 2017b). These movement metrics include *displacement distances* on a daily scale and 10-day scale as well as three recursive movement metrics, including *revisit rates*, *residence time*, and *return time*. The daily displacement is calculated as the distance measured in a straight line between two locations that were recorded at the start and end of a 24-hour period, which shows how far the animal moves in a day. The 10-day displacement is calculated in a similar way as the daily displacements, but with locations at

the beginning and end of a 10-day period instead of a 24-hour period. The advantage of calculating displacements based on GPS positions 10 days apart is that the displacements can serve as a metric of movements over longer timescales and approximate long-distance nomadic movements. The recursive movement metrics are used extensively to quantify how animals exploit resources (Berger-Tal and Bar-David, 2015; Bracis et al., 2018). For each individual, I calculated the recursive metrics for each GPS location in the movement trajectory itself. To assess the revisit rate, residence time, and return time, I centered a 1-km-radius circle on each GPS location along the movement trajectory and determine whether an individual returns to the same location (returns within the same circle over time). If an individual leaves the circle for a short time and comes back to the same circle with an 8-h period, this is not considered a revisit in the analysis. The revisit rate is determined as the total number of visits to previously visited circles. The residence time was measured as the total number of days the individual spends inside a 1-km-radius circle centered on each GPS location across all revisits. The return time was measured as the time between visits. Subsequently, for each individual, I sampled the mean values of each of the metrics for further analysis. Second, to explain any underlying pattern in the dataset of movement metrics across species, I carried out a principal component analysis (PCA) for the above mean metrics. PCA is a widely used technique for summarizing a multivariate dataset into a reduced number of uncorrelated dimensions, while minimizing the loss of information in the original dataset (Peres-Neto et al., 2003). I selected the first PCA that explained 72.9% of the variance in the dataset (Figure 3 in A.3), representing the largest variation among the movement metrics. Lastly, I compiled a 16-day interval MODIS NDVI between 2006 and 2017 across the GSE, which determines the vegetation greenness and/or forage availability. I then conducted a mixed model that showed the relationship between the movement variability derived from the first PCA and the forage availability.

Further details about why I select the 1-km radius and the 8-h threshold, how I assess the movement variability based on the PCA, and how I embedded the variability into a gradient of resource availability across the study system are found in the method section of appendix A.3.

6. RESULTS AND DISCUSSION

6.1 Spatiotemporal dynamics in the foraging habitat of ungulates in unpredictable environments

Previous studies that have examined the drivers of nomadic movements have shown that unpredictable spatiotemporal dynamics of foraging resources can be a driver of wide-ranging nomadic movements in arid and semi-arid landscapes (Jonzén and Knudsen, 2011; Mueller et al., 2008, 2011). Surprisingly, I found no evidence of such spatiotemporal dynamics in the foraging habitat of khulan. The dynamic habitat model, which predicts the spatiotemporal dynamics in khulan summer foraging habitat showed that khulan selected habitats with intermediate values of NDVI (Table 1 in A.1). However, these habitats characterized by intermediate NDVI values did not vary at broad scales over time. This pattern indicates that khulan summer foraging habitat is highly predictable within a season and between years, and thus does not explain why khulan are highly mobile. Overall, it appeared unlikely that broad scale unpredictability of foraging habitats is a driver of the high mobility of khulan in the desert. Instead, I found that the spatiotemporal variability of khulan habitat was associated with locations around water resources in the desert (Figure 4 in A.1), suggesting that unpredictable temporal variability in the availability of water resources rather than the broad scale dynamics of foraging habitats maybe the key driver for the high mobility of khulan in the desert in Mongolia. These results indicate that (i) the long-range nomadic movements of large herbivores in resource-poor arid landscapes are not always directly coupled with the unpredictable dynamics of vegetation productivity over time, and (ii) the movements can also be related to unpredictable temporal changes in water availability, which serves as an alternative driver of the nomadic movements of large herbivores in arid landscapes.

The predictable foraging habitat of khulan might be related to the shrubby desert ecosystem (a mix of small shrubs, forbs, and grasses), where khulan occur (von Wehrden et al., 2012). Khulan as an equid species and non-ruminant hind-gut fermenter is adapted to digest large quantities of low-quality forage (Duncan, 1992). Khulan can therefore forage on the shrubby desert vegetation, unlike smaller antelopes, which are ruminants and depend more on herbaceous vegetation (Fryxell et al., 2004). In addition, shrubby vegetation in drylands shows different responses to rainfall in terms of growth compared to herbaceous vegetation in grasslands (Moreno-de las Heras et al., 2015). Plants in herbaceous steppe habitat typically show quick and intense growth pulses within a short period after rainfall events (Moreno-de las Heras et al.,

2015). The vegetation greenness is here highly variable. The plant green-up in shrubby desert and semi-deserts is associated with longer-term precipitation patterns, and the vegetation greenness is less variable over time (Moreno-de las Heras et al., 2015). Studies conducted on the habitat selection of large herbivores in herbaceous grasslands, including Mongolian gazelle on Mongolia's steppe (Mueller et al., 2008) and saiga antelope on the Kazakh steppe (Singh et al., 2010a), showed that animals select areas with intermediate NDVI values and that these preferred habitats are highly dynamic in space and time. In addition, these studies examined the habitat selection of bovids, ruminants which tend to select forage based on quality rather than quantity (Fryxell et al., 2004). The selection of areas with intermediate NDVI values in these studies is linked to the forage maturation hypothesis (FMH), which predicts that herbivores select an intermediate forage biomass to maximize the net daily energy intake, while lower and higher NDVI values have trade-offs between poor-quality forage and the quantity of forage (Fryxell et al., 2004; Mueller et al., 2008; Singh et al., 2010a). Because in shrubby landscapes, the variability in NDVI is less associated with plant phenology and with khulan as non-ruminant grazers, suggesting that khulan's preference for intermediate NDVI values by khulan is not related to the FMH, rather it is related to preferred habitat types. In the desert, vegetation communities with lower NDVI values may represent poor-quality habitat because they likely feature shrubs interspersed with barren grounds, offering limited forage. Habitat types with higher NDVI values may represent areas with riparian vegetation including a greater risk of predation and higher rates of insect harassment, which khulan should avoid.

6.1.1 Unpredictable changes in water availability as an alternative driver of nomadic movements

The availability of water resources in desert and semi-desert landscapes (e.g. ephemeral oases, wetlands) is highly dynamic – with water resources changing in extent, depth, turbidity, and salinity as they periodically fill and dry and as flood waters flow through the landscape (Dean, 2004; Dean et al., 2009; Roshier et al., 2008b). These unpredictable temporal changes in water availability are known as a driver of the nomadic movements of waterbirds in arid and semi-arid environments. The red-billed teal *Anas erythrorhyncha*, a waterfowl in South Africa shows immediate responses to wetland filling and appears to respond to shifts in resource conditions in a given area (Roshier et al., 2008a). My study shows a similar pattern in which khulan in the Dzungarian desert may track changes in water availability. Previous studies on

equids have shown that they are water-dependent accessing water more or less daily during dry seasons and that the distance to water is an essential factor in habitat selection by wild equids (Kaczensky et al., 2010; Zhang et al., 2015). In addition, I found that the distance to water is a significant factor in explaining khulan habitat selection in the desert, since khulan avoided habitats more than 21 km away from water sources. Thus, khulan seem to be able to use foraging areas up to a maximum of 21 km away from water sources, after which they are forced to either return to the previously visited water source or continue to a different one. The GPS movement data that I used for model validation showed that each khulan used several different water sources located up to 100 km apart from each other across the landscape. Other large herbivores, for example, African savannah elephants *Loxodonta africana* in Namibia's semi-arid ecosystem showed a similar pattern, switching water sources in order to access new foraging areas, which drives their high mobility (Polansky et al., 2015). Thus, the sparsely distributed, spatially patchy and temporally unpredictable water sources can be a landscape-scale driver of nomadic movements for ungulates in resource-poor arid and semi-arid regions. Nevertheless, we are still only at the beginning of our understanding of what possible drivers promote the long-distance nomadic movements of ungulates and under what circumstances. Future studies should further investigate the importance of water sources as a landscape-scale driver of wide-range movements in nomadic animals.

6.2 Nomadic movement patterns and challenges in conserving nomads

Studies on nomadic species have emphasized that the high individual-level variability in nomadic animals, the lack of temporal predictability in nomads' space use, and the nomads' requirement for vast, intact landscapes pose a significant conservation challenge. However, there has been little research on these key movement characteristics for nomadic ungulates, and on their potential implications for the animals' conservation, in large part due to a lack of multi-year movement data. Here, I examined the spatiotemporal dynamics of the space use of Mongolian gazelle, and found three aspects of the spatiotemporal dynamics of space use in their nomadic movements: (i) large individual differences in space use within and between years, (ii) a lack of fidelity to particular areas for key stages in the lifecycle (e.g., calving and wintering), and (iii) extremely large lifetime ranges.

6.2.1 The temporal variability and predictability of space use in nomadic movements

The variability in individual behavior can have widespread effects on intraspecific competition as well as population and community dynamics. As a result the variability in individual behavior, including individual variation in space use, is a key factor in ecology and evolution that should receive greater attention in conservation (Merrick and Koprowski, 2017). This is particularly important for nomadic species that display movement behaviors with large individual differences within and between years. My study shows that there is great individual variability in Mongolian gazelle's space use within a year, with an individual occupying an average range of $\sim 19,000 \text{ km}^2$ ($SD = 9,265 \text{ km}^2$) in a single year – about the size of Kruger National Park in South Africa. Some gazelle moving in the same area had ranges up to six times larger than the others (e.g., $6,431 - 53,422 \text{ km}^2$), indicating large individual behavioral differences (Figure 2 in A.2). This individual difference in space use is similar to the case of partial migrants, where individuals are either migratory or sedentary in the population. Some examples include pronghorn *Antilocapra americana* (White et al., 2007), red deer *Cervus elaphus* (Myserud et al., 2011), and moose *Alces alces* (Rolandsen et al., 2017). However, unlike the case of partial migrants where individuals consistently display one behavior or the other, I did not find any consistency in the extent of nomadic movements for the same individual across years. Instead, I found great variability in the space use of the same individual across different years. Range sizes from one year to the next varied by a factor of three (e.g., from $17,890$ to $53,422 \text{ km}^2$ for one individual or from $12,696$ to $37,447 \text{ km}^2$ for another individual), indicating that individual nomadic animals can exhibit substantial behavioral flexibility over time.

Recent studies on migratory ungulates suggest plasticity of migratory behavior, with individual migrants easily switching between migrant and resident movement strategies (Eggeman et al., 2016). This behavioral flexibility has been linked to species resilience and the ability to adapt to environmental changes. Such behavioral flexibility provides an important adaptive advantage for migrants in response to environmental change (Beever et al., 2017). In marine ecosystems, for instance, some individuals of the northern elephant seal *Mirounga angustirostris* show low fidelity during migration, resulting in greater rewards in terms of mass gain during extreme climatic conditions, which are predicted to occur more frequently in the future due to climate change (Abrahms et al., 2018). To date, the extent of behavioral flexibility in nomadism has not been widely explored in large herbivores, but such work related to

environmental changes is essential for understanding the adaptive capacity of nomadic animals in a rapidly changing world.

Site fidelity, the repeated use of sites for breeding, wintering or foraging year after year, is a widespread behavioral strategy across taxa (Sawyer and Kauffman, 2011). Nevertheless, site fidelity varies along a spectrum that ranges from animals with low fidelity, or unpredictable movements (Wittmer et al., 2006), to animals with strong fidelity that move predictably along the same route year after year (Sawyer et al., 2018). In unpredictable environments like wide-open arid regions, animals tend to show low-fidelity to their key areas and nomads are characterized by weak fidelity strategies for coping with unpredictable changes in their environments (Edwards et al., 2009; Robillard et al., 2018). Similarly, the Mongolian gazelle in my study showed a lack of site fidelity to specific wintering areas, with an average distance of 176 km (SD = 91 km) between wintering areas in different years (Figure 3 in A.2). On the other hand, the areas used by Mongolian gazelle during the calving period, showed less variability, yet the distance between the calving grounds in different years was relatively large (91 ± 49 km), provide little evidence for the existence of the “calving grounds” or seasonal ranges mentioned in the literature (Gunn and Miller, 1986; Ito et al., 2013b; Leimgruber et al., 2001; Olson et al., 2010). The lack of site fidelity to wintering and calving grounds can be rooted in the spatiotemporal distribution of landscape attributes, including shifts in forage availability and shallow snow, as has been also shown for other nomadic species in arid environments (Jonzén and Knudsen, 2011; Roshier et al., 2008b).

6.2.2 Lifetime space use and challenges in the conservation of nomadic ungulates

Knowing how much space an animal uses has critical implications for understanding a species ecological needs and identifying the scale and type of conservation management (Allen and Singh, 2016). Although several different methods have been used to estimate home ranges, autocorrelated kernel density estimation (AKDE) is an advanced approach is probably the most accurate estimation for home ranges based on the autocorrelated GPS movement data to date (Fleming et al., 2015). I used AKDE to estimate the lifetime space use of individual Mongolian gazelle. This method uses a limited amount of tracking data to project the space use into the future assuming the animal continues moving in the same way as estimated (with no change in movement processes). My study showed that the lifetime ranges of individual Mongolian gazelle ranged from 38,100 km² to 167,841 km², indicating that individual Mongolian gazelle had

extremely large estimated lifetime ranges (Figure 2 in A.2). Whereas the average annual range was 19,346 km² (SD = 9,265 km², MCP), the estimated average lifetime range for an individual was 100,800 km² (n = 12, SD = 45,356 km², AKDE), which is half of the population core range of Mongolian gazelle (~200,000 km²) (Fleming et al., 2015). This average lifetime space use for an individual Mongolian gazelle is four times larger than the area covered by ~1.2 million wildebeest *Conochaetus taurinus* during their annual migration through the Serengeti-Mara ecosystem (25,000 km²) (Thirgood et al., 2004) and is about the same size as the total area used by 54 caribou *Rangifer tarandus granti* over four years in the Canadian Northwest Territory (84,543 km²) (Nicholson et al., 2016). However, these estimates for other ungulates in different systems were not calculated with AKDE, and the actual gazelle lifetime ranges may be somewhat smaller than I estimated here, because AKDE does not take barriers into account. In contrast to other species whose home ranges have been estimated by AKDE, the Mongolian gazelle has an extensive lifetime space use. For instance, the estimated home ranges of the Sumatran elephant *Elephas maximus sumatrensis* vary between 274 km² and 1352 km² (Pudyatmoko et al., 2018), whereas the home ranges of the jaguar *Panthera onca* range from 24.7 km² to 1268 km² (Pudyatmoko et al., 2018). To date, estimating the lifetime space use with AKDE has not been widely explored for nomadic species, but such analysis is critical for characterizing nomadic movement patterns across different species and ecosystems as well as for developing conservation strategies for nomads.

Nomadic Mongolian gazelle's lifetime space use of over 100,000 km² together with the individual variation in space use and the low fidelity to calving and wintering area all highlight the importance of landscape permeability and landscape-scale conservation management for nomadic species. With nomadic movements, an entire landscape is interconnected over the course of several years. Thus, for nomadic species, in particular for ungulates, landscape-level management that considers all parts of the landscape is key to ensuring permeability across the entire landscape (Kremen and Merenlender, 2018; Poiani et al., 2000).

Maintaining permeability throughout the entire landscape is critical for nomadic ungulates to cope with the patchy and ephemeral distribution of resources and to avoid adversely affected areas during extreme conditions. Studies on ungulates in arid regions have shown large-scale escape movements during severe climate conditions (Kaczensky et al., 2011a), such as the Mongolian gazelle in my study escaping areas affected by severe snow storms. A key challenge is how permeability across entire landscape can be maintained, especially in the face of

infrastructure development, which can prevent nomadic animals from accessing unpredictable and ephemeral resources and from dealing with unpredictable extreme conditions to find favorable habitats to survive across the landscape.

For Mongolian gazelle and other wide-ranging ungulates around the world, the negative effect of linear infrastructure such as fences, highways, and railroads has been widely observed in barrier effects, which cuts off entire areas of the landscape where animals might have to move to escape harsh conditions or access migration routes and seasonal ranges (Ito et al., 2013a; Wingard et al., 2014; Xia et al., 2007). In my study, Mongolian gazelle cannot cross the fence along the national border (Figure 1 in A.2), and the movements of 80% of the 22 tracked individuals were affected by the border fence (Figure 5 in A.2). When approaching the border fence, the movement behavior of Mongolian gazelle was extremely variable in regard to finding a crossing: some gazelle moved extended periods along the border fence, while others immediately gave up and moved away. In addition, several previous studies have shown that fencing causes high mortality in wide-ranging large mammals throughout Mongolia and Eurasia (Ito et al., 2008; Linnell et al., 2016; Olson et al., 2009b). Migratory ungulates that face habitat fragmentation and barrier effects often exhibit significant population declines or have perished altogether (Harris et al., 2009; Wilcove and Wikelski, 2008).

One mitigation measure for minimizing the landscape-scale impacts of linear barriers on wide-ranging migratory ungulates is identifying suitable design, spacing, and locations for crossing structures and movement corridors along the migration routes are a mitigation measure (Bastille-Rousseau et al., 2018; Sawyer et al., 2012). This conservation mitigation measure relies on areas being repeatedly used by migratory ungulates, which show strong fidelity to routes and seasonal ranges. In contrast, nomadic ungulates are difficult to manage because their key areas and seasonal ranges are neither clearly defined nor do the nomadic ungulates repeatedly use the same locations. In wide-open ecosystems in arid environments, identifying the critical corridors and crossings which nomadic ungulates require is challenging because nomadic populations require large expanses of habitat. In addition, there are no crossing structures that have not been tested for nomadic ungulates around the world, and we do not know whether crossing structures are effective or not.

6.3 Variability in nomadic movement behavior across dryland ungulates

The variability in nomadic movements, especially in nomadic ungulates, has not received much attention in the literature, mostly because movement data across multiple nomadic ungulates in different ecosystems are lacking. I compiled one of the most comprehensive movement data sets of nomadic ungulates to date and compared the movements of four species along a xeric desert to mesic steppe resource gradient in Mongolia's Gobi-Steppe Ecosystem. This study is the first systemic study to determine the variability in nomadic movements of ungulate species across a resource gradient, evaluating differences in forage- and water-driven nomadic movements in the warm, vegetation growing season. I hypothesized that in the desert, where temporally unpredictable but spatially stationary water is a key resource, animals are more water-dependent and may show water-driven nomadism with frequent revisits to spatially fixed resources. In contrast, in the steppe, where foraging resources are often both temporally and spatially variable, animals are less water dependent and may show forage-driven nomadism with infrequent revisits to previously used resources. To evaluate the variability of nomadic behavior across the species, for each individual I measured five movement metrics, including daily displacement, 10-day displacement, revisit rate, residence time, and return time. I then carried out a principal component analysis (PCA) for the above mean metrics to explain any underlying pattern in the dataset of movement metrics across species. To examine whether the gradient from the more mesic steppe to the xeric desert explains any of the variability in movement behavior detected in the PCA, I used linear-mixed effects models to predict the relationship between the NDVI gradient and the variability in movement behavior.

6.3.1 Forage- and water-driven nomadism

The first principal component (PC) 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-day displacement distances (Figure 3 in A.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. The full model with resource availability explained 21% of the variation in movement behavior (marginal $R^2 = 0.21$), with resource availability showing a significant effect (Figure 4 in A.3). The relationship between resource availability and the variability in movement behavior (PC1) was negative, indicating that animals living in the desert that exhibited low vegetation greenness (i.e.

mean NDVI value of 0.09) moved shorter distances with frequent revisits to previously used areas, while animals in the steppe with relatively high vegetation greenness (i.e., with a mean NDVI value of 0.3) moved longer distance with infrequent revisits to previously used areas. For example, Mongolian gazelle in the resource-rich steppe moved nearly three times on average (mean \pm SD, 20.9 ± 10.4 km) than similarly sized goitered gazelle (7.9 ± 7.2 km) in the desert at a 10-day scale. It is important to note that the variability among species in the desert environment was very high, and that khulan performed exceptional long-distance movements in the desert. A more detailed discussion on the variability among species in the desert is covered in section 6.3.2 below (Figure 2 in A.3). Overall, however, this pattern derived from the mixed model supports my hypothesis differentiating forage- and water-driven nomadism, providing evidence that the resource gradient modulates ungulates' movements, from exceptionally long-distance movements with low recursion frequency in mesic grassland habitats to shorter movements with higher recursion frequency in desert habitats.

Resource availability is recognized as a significant factor in determining the variability in movements of large mammalian herbivores as well as size of the herbivores' range (Avgar et al., 2013; Bartlam-Brooks et al., 2013). Macro-ecological research linking resource availability to the movements of large herbivores showed that animals in resource-poor landscapes move almost ten times farther than animals in resource-rich landscapes and suggested that longer movements occur in resource-poor environments (Teitelbaum et al., 2015; Tucker et al., 2018). These macro-ecological studies, however, usually cover a broad gradient from forest to temperate grasslands.

My results from comparing ungulate movements in the grassland steppes and those in the deserts indicate a different relationship between animal movements and resource availability in arid environments in which I compared ungulate movements in the grassland steppes and those on deserts. Along the resource gradient in arid environments, ungulates living in the resource-rich steppe move longer distances without a need to return to previously visited areas than those in the desert with low resources. This suggests that movement behaviors on the micro-scale are more complex than those that result from the macro-scale studies. This contrasting difference is probably linked to search behavior for good forage areas in the spatiotemporally variable mesic grasslands (forage-driven nomadism) versus their return movements to spatially fixed water resources in more xeric drylands (water-driven nomadism).

Evidence from theoretical and empirical research demonstrates the important impact of landscape structure to animal movements: landscapes where resources are spatially variable and

temporally unpredictable generally favor long-distance nomadic movements and low landscape persistence (Mueller and Fagan, 2008). For example, a comparative study on four ungulate species across three continents highlighted the triggering of long-distance nomadic movements through the increasing unpredictability in green vegetation. Other studies of large herbivores have similar findings, with greater movement rates in broad-scale heterogeneous landscape to increase the likelihood of encountering suitable foraging-area locations (Avgar et al., 2013). For Mongolian gazelle, this pattern also applies to movement distance, where broad-scale spatial variability in vegetation is associated with long-distance nomadic movements (Mueller et al., 2011). As the spatial scale of resource variability increases, so does the distance an animal would need to move to reach an area with different resource availability, possibly leading to long-distances as animals track food availability across the year. Simulation studies have also suggested that random search strategies increase encounter rates in patchy and aggregated foraging resources (Raposo et al., 2011). I found that Mongolian gazelle exhibit long-distance movements and low repeatedly used areas. Along with the previously outlined behaviors, ungulates can employ random searches to increase the likelihood of encountering suitable foraging areas in resource-poor arid landscapes, where foraging resources vary on a broader spatial scale and are temporally unpredictable.

In contrast, ungulates in the resource-poor deserts moved shorter distances and showed high repeated use of resources. This pattern could be a result of desert animals' movements mostly being constrained by spatially explicit water resources. Large water-dependent herbivores in many ecosystems fundamentally rely on water resources for survival, which effectively constraints the herbivores' movements, as they must repeatedly return to central water resources (Bleich et al., 2010; Rozen-Rechels et al., 2015). Many studies have shown that animals forage further away from water sources as they deplete the forage in the vicinity of water sources (Giotto et al., 2015; Martin et al., 2015). Eventually, they must return to access water, resulting in a commuting pattern between forage and water resources. One recent study on the role of spatial memory in the movement decisions of wide-ranging elephants in the African savanna has demonstrated that the elephants showed highly directional rapid movements to the closest water sources, suggesting that they possess a detailed spatial memory that allows them to minimize the travel distance to water resources (Polansky et al., 2015). Similarly, desert ungulates may have to range farther in the resource-poor landscape, but they must periodically return to watering areas, leading to water-driven nomadism. My findings support the possibility that mesic to xeric

environmental gradient impacts the ungulates' return movements. However, due to the broad scale of the study region and its sparsely distributed ephemeral water sources, I could not explicitly confirm that the recorded recursive movements were those of ungulates returning to water sources. Overall, my study sheds new light on the importance of considering the variability of nomadic movements in arid regions and suggests that understanding the spatiotemporal predictability of key nomadic movement drivers across different ecosystems is essential in identifying different movement strategies. In addition, the difference in forage- and water-driven nomadic movements is important information that can inform conservation strategies: Forage-driven nomads primarily require a high degree of landscape-level permeability, and water-driven nomads also require the protection of ephemeral water bodies as well as measures to maintain the functional connectivity between the water bodies.

6.3.2 Variability in movements across species

The movement behaviors observed in my study varied significantly for species in the xeric desert environment (Figure 2 in A.3). For both daily and 10-day displacements, goitered gazelle had the highest mean revisits and residence time and the shortest displacement distance, indicating goitered gazelle return often to only a few specific areas. In contrast, the saiga antelope, a similarly sized ungulate in the desert, is more mobile and returned less frequently to previously used areas. This difference between goitered gazelle and saiga antelope in the desert suggests that goitered gazelle could be more water-dependent than saiga antelope. Several studies have reported water to be an important resource for saiga antelope (Bekenov et al., 1998; Singh et al., 2010b). However, the saiga antelope's water usage and its impacts on their movements require further investigation. Based on the khulan's movement behavior with very long movement distances and few revisits to previously used areas, khulan appear to be highly mobile. As an equid species, khulan require more or less daily access to water sources, making the distance to water is an essential factor in habitat use (Buuveibaatar et al., 2016a; Kaczensky et al., 2010). It is possible that in the desert, the high mobility of khulan may be triggered by ephemeral water holes, which are excavated by khulan in depressions, allowing them to forage further than would be possible with spatially fixed water sources (Feh et al., 2001). In the first research question in this thesis, I suggested that khulan return to sparsely distributed small springs and large oases, whose locations are spatially static, but availability of water at these locations is

temporally unpredictable (A.1). In contrast, goitered gazelle might rely only on permanent water sources because they are unable to excavate depressions to make ephemeral watering holes.

7. CONSERVATION IMPLICATIONS AND FUTURE PERSPECTIVES

Many nomadic species require urgent conservation attention, yet the current lack of long-term robust data about nomadic animal movements is a serious impediment in developing data-driven effective conservation measures. As the field of movement ecology continues to develop, it is important to strengthen its link with animal conservation to support better implementations of evidence-based conservation actions.

By using multi-year monitoring data to characterize the movements of nomadic ungulates, I provided new insights into nomadic ungulate movements in arid and semi-arid regions, namely: (i) the temporal variability in water resources is an alternative driver of nomadic movements in ungulates; (ii) nomadic ungulates are characterized by large lifetime ranges and a lack of fidelity to their breeding and wintering areas, while individuals show great behavioral flexibility in space use within and between years; and (iii) there is significant variability in nomadic movements depending on landscape attributes: water-driven nomads in xeric habitats repeatedly use certain areas, whereas forage-driven nomads in more mesic habitats in drylands generally do not return to previously used areas. These findings together highlight the importance of multiple-year monitoring data for characterizing nomadic movements and providing a means to better understand the challenges in the conservation of nomadic ungulates.

Studies on wide-ranging species have established that spatially static protected areas (PAs) are not the most effective conservation measure. For wide-ranging species, where PAs alone are not sufficient for the species' conservation, a number of dynamic conservation concepts have been suggested: (i) mobile PAs (Taillon et al., 2012), (ii) PA networks (Roshier et al., 2002; Singh and Milner-Gulland, 2011), and (iii) biodiversity offsets (Bull et al., 2013; Gordon et al., 2015). Both mobile PAs and PA networks depend upon locations that are known to be important at some point throughout the year, while biodiversity offsets are location-based approaches based on the underlying idea that detrimental landscape modifications can be offset by conservation measures in different, spatially distinct areas compared to the area of impact. Like other wide-ranging species, such as migratory ungulates, nomadic ungulates use large expanses of area that far exceed the size of available static PAs, which makes the use of static PAs alone ineffective for nomadic ungulate conservation. Furthermore, the space use pattern of nomadic ungulates is

characterized by their unpredictability, indicating that nomadic ungulates lack fidelity to movement corridors and that the permeability across the entire landscape is a critical requirement for their survival. Any of the three aforementioned dynamic approaches, however, are location-based and depend on the knowledge that a particular area will be important for the focal species during at least some portion of the year. This means while these approaches can be important components of a conservation strategy for nomadic ungulates, broad-scale landscape management which considers permeability across the entire landscape should be a key component of conservation management for nomadic ungulates.

Importantly, however, different drivers of nomadic movements, such as water and forage resources, can promote different types of nomadic movements. My study showed the difference between the nomadic movements of water- and forage-driven nomadic animals living in the xeric desert and mesic steppe. Such behavioral differences among nomads suggest that individual nomadic animal species may require different conservation strategies. Forage-driven nomadic animals with long-distance movements and few repeatedly used areas may benefit most from landscape permeability and protective measures at the landscape scale, whereas water-driven nomadic animals with shorter-distance movements and repeatedly used areas may require landscape permeability as well as mostly functional connectivity between water resources.

Conservation efforts aimed at protecting wide-ranging species face serious challenges across the globe, including habitat loss, fragmentation, and climate change (Collingham et al., 2004; Tucker et al., 2018). A growing body of literature emphasizes that global warming will drive changes in precipitation and increase the frequency and severity of extreme climatic events (Diffenbaugh et al., 2017; Duncan et al., 2012). Consequently, landscape permeability will be even more essential for the survival of nomadic animals if they should ever need to escape severe conditions and move to novel locations. Therefore, any landscape-scale impacts of linear infrastructure, including fences, highways and railroads, which bisect habitats, should be avoided or minimized in wide-open arid and semi-arid regions where nomadic ungulates occur. Where linear infrastructure cannot be rerouted to avoid conflict, due to the lack of fidelity in nomadic movements, I recommend that crossing options must be frequent along railroads or fences, similar to the high density of crossing options in other successful mitigation measures for migratory ungulates.

Integrating knowledge about the spatial and temporal variability and predictability of animal movements (e.g., identifying patterns in animals' space use, key areas, connectivity

among habitats, and animals' exposure to other threats) into conservation planning for nomadic species is challenging but critical in establishing effective conservation measures. To address this challenge, it is essential to prioritize the collection of both long-term fine-scale movement data and environmental data with the aim of quantifying animal movement patterns as well as environmentally assessing development projects. In the absence of such information, many knowledge gaps for nomadic animals will continue to be unaddressed, resulting in ineffective conservation actions. I believe it is important that conservationists recognize the limitations of using scientific evidence about nomadic animals derived from short-term data or single-year studies and to develop conservation plans that account for landscape permeability for nomadic species wherever possible. In addition, I emphasize that a longer-term and higher resolution dataset on the movements of nomadic species would be helpful to better detect spatiotemporal patterns in the variability of movements. Such data would allow researchers to examine whether nomadic animals use long-term memory and return to previously visited areas over years (e.g., seasonal and/or between-year returns). These types of studies would be important to identify whether nomadic ungulates have refuge areas, which they reuse during extreme climatic events, such as is observed in nomadic birds, or whether they exhibit any fidelity to their movements across years. The multiple-year monitoring dataset would also allow researchers to demonstrate how nomads know when and where to go, how nomads can find suitable conditions in wide-open intact regions, and how far away they detect suitable conditions. To date, few studies have examined such questions across multiple species or multiple populations. In addition, movement studies on nomads to date have rarely explored the role of nomadic movements in shaping population abundance. Ultimately, movement data will need to be coupled with robust population censuses to understand how demographic processes are linked to space use. The long-term movement data on nomadic ungulates collected in my study and the resulting insights into the differing movement patterns of nomadic ungulates under different landscape and resource conditions are a first step, and future research should be directed to increase the effectiveness of conservation strategies for nomadic ungulates in highly dynamic arid and semi-arid regions.

8 ZUSAMMENFASSUNG*

Neuere Studien zur Bewegungsökologie von Tieren haben gezeigt, dass große herbivore Säugetiere in ressourcenarmen und trockenen Umgebungen eher nomadische Langstreckenbewegungen durchführen als regelmäßige saisonale Wanderungen zu vollbringen.

Einige Studien haben diese nomadischen Bewegungen bereits mit den räumlichen Variabilität und zeitlichen Unvorhersagbarkeit von Nahrungsressourcen in der Landschaft in Verbindung gebracht. Während Migration gut untersucht ist, gibt es nur wenige Fallstudien für nomadische Huftiere in Bezug auf die Ursachen nomadischer Bewegungen und die Variabilität der Bewegungsmuster. Darüber hinaus haben zahlreiche Studien gezeigt, dass eine der wichtigsten Herausforderungen bei der Erhaltung hochmobiler Arten darin besteht, die Unvorhersehbarkeit ihrer Langstreckenbewegungen zu berücksichtigen. Dies gilt insbesondere für nomadische Langstreckenbewegungen. Traditionelle Schutzmaßnahmen wie beispielsweise die Erhaltung von Migrationskorridoren, Reproduktions- oder Überwinterungsgebieten, die für die klassische, regelmäßige Migration entwickelt wurden, werden bei nomadischen Arten unwirksam, da deren Bewegungen sehr variabel sind und kritische Bereiche, einschließlich Brut- und Überwinterungsgebiete, zwischen den Jahren variieren. Das Gobi-Steppe Ökosystem in der Mongolei, eine weit offene, trockene Landschaft, bietet eine große Vielfalt an Wildtieren, darunter Huftierarten in weit offenen Steppen und Wüsten wie die mongolische Gazelle (*Procapra gutturosa*), die Kropfgazelle (*Gazella subgutturosa*), die Saiga-Antilope (*Saiga tatarica mongolica*) und den asiatischen wilden Esel (*Equus hemionus*; Khulan auf Mongolisch). Diese Huftiere im Gobi-Steppe Ökosystem wandern über weite Strecken als Teil einer nomadischen Bewegungsstrategie, die ihre zahlreichen Populationen aufrecht erhält, indem sie ihnen Zugang zu den besten, räumlich und zeitlich sehr dynamischen Ressourcen gewährt. Das Ökosystem Gobi-Steppe ist daher eine der wenigen Regionen, in denen die nomadischen Bewegungen von Huftieren erforscht werden können.

Das übergeordnete Ziel meiner Doktorarbeit war es, die räumlich-zeitliche Variabilität der Bewegungen von nomadischen Huftieren im mongolischen Gobi-Steppe Ökosystem zu untersuchen und zu quantifizieren, um die möglichen Treiber und Charakteristika solcher Bewegungen besser zu verstehen und die besonderen Herausforderungen zu untersuchen, die mit dem Schutz und Erhalt nomadischer Bewegungen verbunden sind. In dieser Arbeit habe ich einen konzeptionellen Rahmen entwickelt, der sich auf die Schlüsselmerkmale von Nomadenbewegungen konzentriert, um drei Hauptforschungsziele zu untersuchen: (i) die umweltbedingten Ursachen nomadischer Bewegungen, (ii) die zeitliche Dynamik der Raumnutzung und (iii) die Variabilität nomadischen Bewegungsverhaltens zwischen Huftieren und Ökosystemen. Darüber hinaus verknüpfte ich die wichtigsten Ergebnisse mit bestehenden Schutzkonzepten für sehr mobile Arten und stellte eine Abschlusssynthese zur Verfügung. Die

Ergebnisse meiner Forschung tragen zur weiteren Entwicklung von Erhaltungskonzepten für nomadische Arten bei, die für den Fortbestand des Nomadismus und die Bewahrung der Bewegung als Verhaltensphänomen unerlässlich sind.

Für das erste Forschungsziel verwendete ich einen bodengestützten Line-Transect Langzeitdatensatz mit Daten zu Khulans und Kropfgazellen, welcher von Forschern und Rangern der Great Gobi Strictly Protected Area zusammengestellt wurde. Der Datensatz umfasst 12 Studien, die zur Überwachung der Verbreitung und des Vorkommens von Khulans, einer sehr mobilen Huftierart, und Kropfgazellen zwischen 2004 und 2009 monatlich durchgeführt wurden. Somit standen mir Daten von insgesamt 22894 Kuhlans in 723 Herden sowie 5387 Kropfgazellen in 1136 Herden zur Verfügung. Um zu überprüfen ob raumzeitliche Dynamiken der Nahrungshabitate des Khulans in der Tat die wahrscheinlichsten Ursachen ihrer nomadischen Bewegungen sind, sagte ich geeigneten Khulan-Lebensraum in bestimmten Jahreszeiten und zwischen Jahren vorher. Hierbei nutzte ich satellitengestützte Daten des Normalized Difference Vegetation Index (NDVI), um die Produktivität der Vegetation im Studiengebiet zu erfassen und ein dynamisches Habitatmodell zu erstellen. Dieses zeigte die Eignung der Studienregion als Khulan-Habitat in 16-Tage-Intervallen in den Sommern von 2004 bis 2009 in insgesamt 42 Prognosekarten an.

Meine Analyse zeigte, dass die Futterhabitate des Khulans während der Sommermonate sehr gut vorhersagbar waren und weder räumlich noch zeitlich stark variierten. Die wenigen und kleinen Gebiete, welche hohe Eignung als Habitat für Khulans zeigten, befanden sich in der Nähe von Wasserstellen, zudem vermieden Khulans Gebiete die weiter als 21 Kilometer von einer Wasserstelle entfernt waren. Diese Ergebnisse deuten darauf hin, dass nicht die zeitlichen Veränderungen der Futterhabitate, sondern die zeitlichen Veränderungen der Wasserverfügbarkeit die Hauptursache für die außerordentlichen Langstreckenbewegungen des Khulans in der Wüste Gobi darstellen könnte. Dieses Hauptergebnis liefert neue Einblicke in die Ursachen eines der am wenigsten verstandenen Tierbewegungsmuster und verbessert außerdem das Verständnis für die räumlich-zeitlichen Ursachen nomadischer Tierbewegungen. Zudem unterstreichen meine Ergebnisse die Wichtigkeit zugänglicher und miteinander verbundener Wasserstellen für wilde Huftiere in Trockengebieten.

Für das zweite Ziel habe ich zusammen mit Kollegen einen mehrjährigen GPS-Bewegungsdatensatz zu mongolischen Gazellen in der mongolischen Steppe gesammelt. Hierzu habe ich zwischen 2014 und 2015 22 Individuen mit GPS-Sendern ausgestattet und deren

Bewegungen über einen Zeitraum von ein bis drei Jahren verfolgt. Mit 12.166 täglichen GPS-Positionen stellt dieses Datenset das derzeit größte Langzeitdatenset mongolischer Gazellen dar. Anhand dieser Daten, welche einzigartige Einblicke in das Verständnis der Raumnutzungsmuster von Nomadenbewegungen und deren Auswirkungen auf Erhaltungsmaßnahmen boten, untersuchte ich die Variabilität und Vorhersagbarkeit der Raumnutzung nomadischer mongolischer Gazellen über mehrere Jahre hinweg und verglich deren Bewegungen mit simulierten Gazellenbewegungen. Zudem untersuchte ich den Einfluss von Schutzgebieten, Gebieten hoher menschlicher Landnutzung (beispielsweise Ölfelder) und Infrastrukturbarrieren (beispielsweise Grenzzäune) auf die Bewegungsmuster der besenderten Individuen.

Meine Ergebnisse zeigten eine ausgeprägte individuelle Variabilität der Raumnutzung innerhalb und zwischen verschiedenen Jahren mit besonders hoher Unvorhersagbarkeit an Überwinterungs- und Kalbungsorten. Diese Unvorhersehbarkeit der Raumnutzung führte zu einer geschätzten individuellen jährlichen Raumnutzung von ca. 19000km² sowie einer geschätzten lebenslangen Raumnutzung von 100,000 Quadratkilometern. Hierbei ist von großer Bedeutung, dass bestehende Schutzgebiete bei der Raumnutzung der mongolischen Gazelle nur eine untergeordnete Rolle spielten. Jedes einzelne Schutzgebiet in der Studienregion ist zu klein um selbst die jährliche Raumnutzung einer einzelnen Gazelle abzudecken. Zugleich mieden die Gazellen Gebiete mit hoher menschlicher Landnutzung, beispielsweise Ölfelder. Aufgrund ihrer weitläufigen Bewegungen waren mongolische Gazellen besonders von durch Infrastruktur verursachten Barrieren betroffen. Die im Studiengebiet befindlichen Grenzzäune beschränkten die Bewegungen von rund 80% aller untersuchten Individuen. Nachdem sie auf einen Grenzzaun trafen, legten Gazellen eine mittlere Entfernung von 11 Kilometern entlang des Zauns zurück. Dies deutet darauf hin das häufige Überquerungsmöglichkeiten nötig sind um die Durchlässigkeit dieser Barrieren zu gewährleisten. Meine Ergebnisse zeigten dass für Huftiere, deren Flächennutzung über Jahre stark variiert, mehrjährige Bewegungsdaten für eine solide Erhaltungsplanung unerlässlich sind. Zudem betonten sie, dass ortsbasierte Schutzmaßnahmen alleine nicht ausreichend sind um diese Arten zu erhalten. Die Überwindung von Infrastrukturbarrieren ist hierbei von besonderer Bedeutung. Da nomadische Tierarten keine festen Bewegungskorridore unterhalten, befürworte ich einen Ansatz auf Landschaftsebene und unterstreiche die Bedeutung der Landschaftspermeabilität für die Erhaltung von nomadischen Arten in Trockengebieten.

Für das dritte Forschungsziel verwendete ich bereits vorhandene GPS-Bewegungsdaten von vier Huftierarten (Khulan, mongolische Gazelle, Kropfgazelle und Saiga-Antilope) mit insgesamt 40 besenderten Individuen, um die Variabilität von deren Bewegungsverhalten im mongolischen Gobi-Steppe Ökosystem zu quantifizieren. Hierbei untersuchte ich Unterschiede bei durch Wasser- und Nahrungssuche getriebenen nomadischen Bewegungen entlang eines Ressourcengradienten von mesischer Steppe zu xerischen Wüstengebieten. Hierzu berechnete ich die zurückgelegten Distanzen sowie mehrere Rekursionsmetriken aus den verwendeten GPS-Daten. Zudem quantifizierte ich die Variation in den Bewegungsmustern mithilfe einer Hauptkomponentenanalyse und unter Nutzung des normierten differenzierten Vegetationsindex als Proxy für den Ressourcengradienten.

Ich konnte zeigen, dass unter verschiedenen Umweltbedingungen verschiedene nomadische Bewegungsstrategien genutzt wurden. In der ressourcenreichen mesischen und semi-ariden Steppe, die durch räumliche Variabilität und zeitliche Unvorhersehbarkeit von Nahrungsressourcen gekennzeichnet ist, legten die untersuchten Arten außergewöhnlich lange Strecken zurück, ohne bestimmte Bereiche häufiger zu nutzen als andere. In ressourcenarmen xerischen Wüstengebieten hingegen sind weiträumige Nahrungsressourcen weniger variabel. Hier dienten räumlich vorhersagbare und zeitlich nicht vorhersagbare Wasservorkommen als Haupttreiber nomadischer Bewegungen. Diese Wasserquellen beschränkten Wanderbewegungen und verursachten eine gehäufte Nutzung bestimmter Gebiete. Beispielsweise legten mongolische Gazellen in der Steppe fast dreimal so große Distanzen zurück als gleich große Kropfgazellen in der Wüste, gemessen in zehntägigen Intervallen. Zudem unterschieden sich die Bewegungsmuster in Wüstengebieten signifikant zwischen den untersuchten Tierarten. Während Kropfgazellen häufig zu bereits genutzten Bereichen zurückkehrten und dazwischen nur geringe Strecken zurücklegten, wiesen ähnlich große Saiga-Antilopen in der Wüste eine höhere Mobilität und geringere Standorttreue auf. Khulans zeigten in der Wüste ebenfalls eine geringe Standorttreue und legten weite Strecken zurück. Diese Variabilität der Bewegungsmuster zwischen verschiedenen Tierarten könnte auf Unterschiede in der Wasserabhängigkeit dieser Arten hin deuten, da sich diese physiologisch und in ihren Strategien zur Wassergewinnung unterscheiden. Meine Ergebnisse haben wichtige Auswirkungen auf Erhaltungsstrategien für nomadische Huftierarten: Nahrungsgetriebener Nomadismus erfordert eine hohe Durchlässigkeit der Landschaft, während für den wassergetriebener Nomadismus zusätzlich auch der Schutz

kurzlebiger Wasserquellen sowie die Erhaltung der funktionellen Konnektivität dieser Wasserstellen unabdingbar ist.

Meine Forschung leistet drei Hauptbeiträge zum besseren Verständnis nomadischer Huftierbewegungen in Trockengebieten: (i) die zeitliche Variabilität von Wasserressourcen ist ein alternativer Treiber nomadischer Bewegungen von Huftieren; (ii) nomadische Huftiere sind durch weite lebenslange Raumnutzung und eine fehlende Treue zu Reproduktions- und Wintergebieten gekennzeichnet, während Individuen eine große Flexibilität in Bezug auf ihre Raumnutzung während des Jahres und zwischen verschiedenen Jahren aufweisen; und (iii) nomadische Bewegungen variieren abhängig von Landschaftseigenschaften: Wassergetriebene Nomaden in xerischen Habitaten nutzten bestimmte Bereiche häufiger, während Nahrungsgetriebene Nomaden in mesischeren Habitaten in Trockengebieten nicht zu bereits genutzten Gebieten zurückkehrten.

Die Ergebnisse meiner Doktorarbeit unterstreichen die Bedeutung mehrjähriger Bewegungsdaten sowohl für die Charakterisierung von Nomadenbewegungen als auch für die Planung von Strategien zur Erhaltung nomadischer Huftiere. Nomadische Huftiere können in ortsbasierten Schutzgebieten nicht effektiv geschützt werden, stattdessen müssen ihre Bedürfnisse in die Landschaftsplanung einbezogen werden, wobei die Landschaftspermeabilität besonders berücksichtigt werden muss. Für futtergetriebene Nomadentiere, die eine geringe Rekursion aufweisen, muss die Durchlässigkeit in der gesamten Landschaft das Hauptanliegen sein. Für wassergetriebene Nomadentiere sind die Durchlässigkeit der Landschaft sowie die Verteilung von Wasserstellen und deren funktionale Konnektivität ein Hauptanliegen für die Aufrechterhaltung der Nomadenbewegungen in trockenen Landschaften.

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11 APPENDICES

A.1 Spatiotemporal habitat dynamics of ungulates in unpredictable environments: The khulan (*Equus hemionus*) in the Mongolian Gobi desert as a case study

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(2) Conducting tests and experiments

Doctoral candidate ND 50% (water resource data collection and compiling a long-term dataset)

Co-authors OG and PK 50% (collecting wildlife transect and also GPS movement data)

(3) Compilation of data sets and figures

Doctoral candidate ND 100% (cleaning up the data, measuring the relevant static and environmental variables for constructing a habitat model and preparing all figures).

(4) Analysis and interpretation of data

Doctoral candidate ND 75% (all statistical analyses including spatial models, regression analyses and the interpretation of data).

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with the spatiotemporal unpredictability of foraging resources in a highly dynamic landscape (Mueller et al., 2008). Although highly mobile nomadic movements within seasons have been described in several other species or populations (Roshier et al., 2008; Singh et al., 2012; Taillon et al., 2012), the concept and its drivers remain poorly understood and little studied. In addition, nomadic species require large, unfragmented habitats. This is crucial for them to be able to move freely to respond rapidly to shifting resource availability and changing conditions over time and to cope with unpredictable resource distribution (Dean, 2004; Jonzén and Knudsen, 2011). Consequently, conserving nomadic species is a key challenge for identifying the scale of conservation management and designing conservation actions. Recent studies suggest that understanding patterns, dynamics and drivers of high mobility of animals could inform the relative importance of landscape connectivity that link important habitats or resources (Allen and Singh, 2016; Jacoby and Freeman, 2016).

The Gobi desert of Mongolia is a portion of the Central Asian Desert ecoregion often characterized by lack of surface water and predominance of low-productivity foraging resources (von Wehrden et al., 2012). It provides an important refuge for several large and wide-ranging ungulates, including the largest population of Asiatic wild ass, or khulan (*Equus hemionus*, henceforth referred to as khulan) in the world (Kaczensky et al., 2015a). While khulan are highly mobile, performing extremely long-range movements in relatively short time periods, they have no distinct migratory pattern (Kaczensky et al., 2006). In most regions of the Gobi, distribution and habitat use of ungulates are heavily affected by humans and their livestock, making it difficult to disentangle the effect of habitat use and human influence. In our study area however, the Great Gobi B Strictly Protected Area in the Dzungarian Gobi (the study area, henceforth referred to as the Dzungarian Gobi), humans and their livestock leave the protected area in summer, thus khulan spatial distribution can be expected to be primarily driven by landscape dynamics in this season. A variety of anthropogenic threats, mainly linear barriers through infrastructure projects, poaching, and competition with livestock for water sources and pasture, have resulted in khulan being listed as “Near Threatened” in the IUCN Red List (Kaczensky et al., 2015b) and if khulan mobility is linked to unpredictable resources, anthropogenic factors may impede the mobility and reduce the population viability. Hence, identifying the main drivers of their mobility is a management priority.

In this study, we determine the environmental factors predicting khulan presence during the summer vegetation period and subsequently examine the intra and inter-annual dynamics of the predicted khulan summer foraging habitat. Our habitat model and the derived prediction surfaces are built on six years of khulan occurrence data from ungulate surveys, a dynamic habitat variable based on remotely sensed imagery of vegetation productivity (Normalized Difference Vegetation Index, NDVI), and several static habitat variables (elevation, slope, distance to water and protection status). We expected that (a) vegetation productivity would be a main driver of khulan spatial distribution patterns; and (b) that khulan presence probability surfaces (subsequently also referred to as “summer foraging habitat”) would be highly variable within and among years due to high spatiotemporal variation in vegetation productivity, and thus could be a key driver for the long-range movements of khulan in the Dzungarian Gobi during summers. Our study is one of the first to examine dynamics of foraging habitat for a highly mobile species in a desert ecosystem.

2. Materials and methods

2.1. Species and study area

Khulan are one of seven wild equid species. They are predominantly grazers in summer, but also consume considerable amounts of shrubs in winter (Xu et al., 2012). As hind-gut fermenters they rely on a higher intake rate and forage abundance than ruminants in order to meet their

nutrient requirements and maximize energy (Janis, 1976). With an estimated 40,000 individuals, the Mongolian Gobi desert provides critical habitat for the largest remaining population of khulan (Buuveibaatar et al., 2016b). However, a substantial portion of the khulan’s range is under consideration for economic infrastructure development which may result in habitat deterioration, loss, and fragmentation (Batsaikhan et al., 2014; Ito et al., 2013). Khulan annual ranges vary regionally between 4500 and 70,000 km² (Kaczensky et al., 2011, 2006).

We conducted our study in the Great Gobi B Strictly Protected Area in the Dzungarian Gobi of southwestern Mongolia. The protected area covers 9000 km² plus a 5700 km² buffer zone, with elevations ranging from 1000 to 2900 m asl (Fig. 1). The protected area was established in 1975 to conserve semi-desert and desert ecosystems and their associated biodiversity, including several endangered ungulates such as about 5700 khulan and 5900 goitered gazelle *Gazella subgutturosa*, which are the two most abundant wild ungulates in the Dzungarian Gobi (Ransom et al., 2012). The area is bordered by the Altai Mountains in the north, and several high mountains (2500–2900 m) along the border with China in the south. Although the international border is fenced, the rest of the protected area is not surrounded or dissected by fences.

Most water sources are located in the foothills of the mountains, but underwater run-off channels also feed multiple springs in the plains and rolling hill country. Thus, the study area is characterized by sparsely distributed water sources, which in some places form oases, as well as ephemeral dry river beds and drainages. The study area has a continental climate with a mean annual temperature of -1.3°C , varying from $+35^{\circ}\text{C}$ in summer to -43°C in winter (Kaczensky et al., 2015a). The average annual precipitation is <100 mm with more than half of the precipitation occurring from June to August. Consequently, the growing season and greenest vegetation period (hereafter: vegetation period) lasts from June until mid-September.

Vegetation communities follow an elevational gradient (von Wehrden et al., 2006). High elevations (above 1800 m) are dominated by perennial grasses and sedges. Steep hills are almost devoid of vegetation with few perennial grasses. Intermediate elevations are characterized by desert-steppe with a high proportion of mixed shrub-grass communities, including shrubby *Salsola* spp. and *Anabasis* spp., the shrub *Haloxylon ammodendron* and *Stipa* spp. grasses. Depressions in the central part of the study area have unevenly scattered shrubs such as *H. ammodendron* and *Nitraria sibirica* (von Wehrden et al., 2006) interspersed with large patches of barren ground. Relatively high-productivity riparian vegetation communities are rare and restricted to larger oases and intermittently dry river valleys.

Due to its distance from population centers, the study area is subjected to relatively low human impact. In summer, human and livestock presence in the study area is minimal as herders move to the more productive summer pastures in the foothills and alpine meadows of the Altai Mountains.

2.2. Ground surveys

Between October 2003 and October 2010 Great Gobi B Strictly Protected Area staff conducted 33 ground-based surveys to monitor ungulates following a distance sampling approach (Kaczensky et al., 2015a). For this study, we used the 12 surveys conducted during the vegetation period (June–September) from 2004 to 2009.

A survey team consisted of four people (driver, observer, and two spotters with compasses) recruited from the park rangers and administration staff; driving speed was 40 km/h. Given the ruggedness of the topography (hills and shrub-covered depressions), we could not use a random or systematic survey design, but rather made use of an existing dirt track system. The survey consisted of 43 transect lines varying in length between 1.5 km and 32 km resulting in a total survey effort of 762 km. Surveys were attempted once a month (Table A.1), and the transects covered the entire protected area (Fig. 1).

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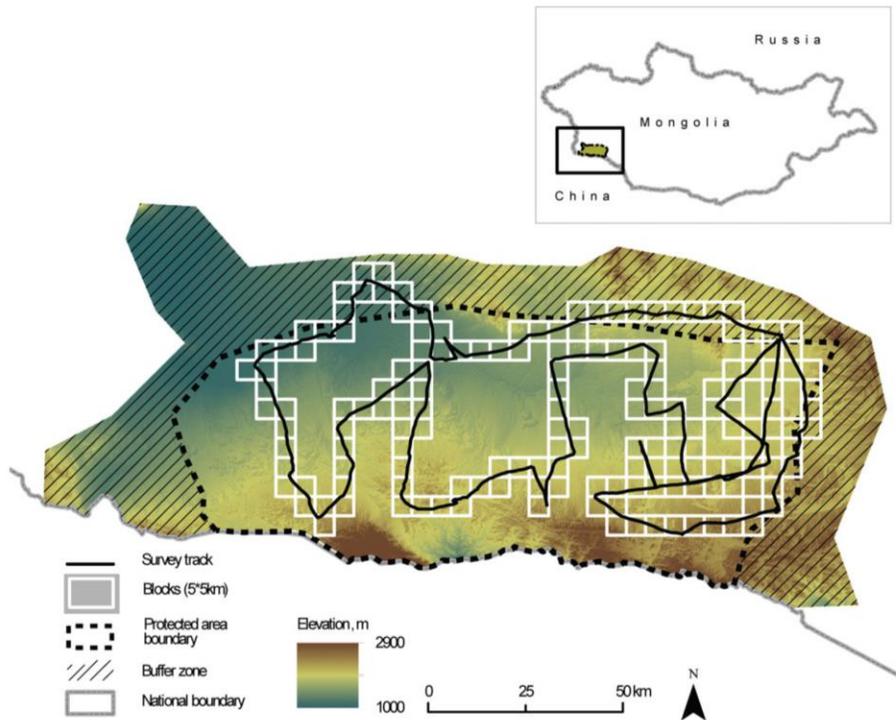


Fig. 1. The Great Gobi B strictly protected area and its buffer zone in the Dzungarian Gobi, Mongolia. Solid black lines indicate survey transects and white lines corresponding survey blocks that were used to summarize census data along the survey transects.

When a group of khulan or goitered gazelles was detected, observers recorded species, group size and their own location, observer distance to animal, and sighting angle using global positioning systems (GPS), and compass bearing respectively. Observers were repeatedly trained to visually estimate distances by placing people at intervals of 100, 500, 1000, 2000, 3000 and 5000 m. Species groups were defined as several animals standing or running in close proximity; no mixed species groups occur. Visibility in the study area is high due to extremely flat topography without steep depressions that would obstruct the observers view. We subsequently calculated the locations of detected khulan and goitered gazelle using geosphere library in R (Robert et al., 2016).

In total, we recorded 22,894 individual khulan in 723 groups and 5387 goitered gazelles in 1136 groups during summer surveys 2004–2009 (Table A.2). Most khulan groups consisted of <10 individuals, though we also recorded a few very large groups (> 500). The range in khulan group sizes varied from 1 to 2110 with a median of 64. This high variation in the abundance data makes models vulnerable to outliers and extreme values and we therefore converted khulan abundance into presence-absence data. Based on GPS tracking data of six khulan in the study area, the average daily displacement of khulan was 6 km. Given this khulan daily movement, we used 5 km² blocks to examine the relationship between khulan presence-absence and environmental covariates. To divide the survey tracks into 5 km² blocks we used the 'XTools Pro' extension in ArcGIS 10.2 (Fig. 1). The length of the survey tracks varied between 714 and 877 km in response to varying dirt road conditions. Thus the total number of blocks varied from survey to survey (ranging between 153 and 191 blocks). A total of 295 khulan observed in 13 groups were excluded from analysis as their positions fell outside the 5 km² blocks. The final analysis is based on 710 groups (totaling 22,599 khulan) (Table A.2). Among individual surveys the number of blocks with khulan presence ranged from 17 to 53 (Table A.2);

blocks were assign absence (0) or presence (1) for khulan and goitered gazelles.

2.3. Dynamic and static covariates

We used static and dynamic environmental covariates in our model. We used the Normalized Difference Vegetation Index (NDVI) as a dynamic measure of vegetation productivity. NDVI is commonly used to monitor large-scale primary production dynamics over time and has proven a valuable index of resource availability and distribution of large herbivores (Pettorelli et al., 2011). Particularly in deserts and grasslands NDVI has been used as a direct indicator of forage availability and quality (Marshal et al., 2006). In our study region, the Gobi desert, NDVI has been shown as a good indicator of vegetation green up and indicator for spatiotemporal variability of foraging resources (Vandendorj et al., 2015).

For each of the survey periods, we used composite MODIS (moderate-resolution imaging spectroradiometer, available at <http://reverb.echo.nasa.gov/reverb>) NDVI images compiled over 16-day intervals at a spatial resolution of 500 × 500 m (Table A.1). For our analysis, we used the seven composites within each summer vegetation period from 2004 to 2009. As static environmental covariates, we used: (i) distance to water, calculated from 80 GPS points for water sources, (ii) a digital elevational model (DEM at 90-m resolution) acquired from Surface Radar Topography Mission (SRTM) data, and (iii) slope (°) calculated from the DEM using 'Spatial Analyst' extension in ArcGIS 10.2. We extracted the mean value of these variables for each survey block. We additionally included presence-absence data of goitered gazelle to test for potential interaction effects and classified survey blocks in protected area versus buffer zone to test for protection status in our model (Fig. 1).

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2.4. Model development

We built logistic mixed (GLMM) habitat models based on the dynamic and static covariates to determine which variables have an effect on khulan habitat selection. To account for spatial autocorrelation, we calculated the proportion of neighboring blocks with khulan presence up to a Euclidean distance of 30 km from each block. To account for varying survey efforts among blocks we included the length of the survey track within each block. We standardized all covariates using a standard deviation of 1 and mean of 0.

To avoid sample asymmetry, we followed procedures in (Mueller et al., 2008) and randomly subsampled the blocks which had khulan absence to equal the number which had khulan presence for each survey. The model used khulan presence-absence as the response variable and included the twelve survey dates and the identifier of each 5 km² block as random effects. We used Restricted Maximum Likelihood to fit our model (REML, lme4 library in R) (Bates et al., 2015), and the Akaike information criterion (AIC) for model selection.

We subsequently built a reduced generalized linear model (GLM) by eliminating the presence-absence of goitered gazelle, the spatial autocovariate, and the length of the survey track from the full model. This reduced model was used to predict the probabilities of khulan occurrence and assess the habitat dynamics across the entire six years, including periods for which we did not have survey data (and thus could not calculate the eliminated variables). This model was also used for model validation with khulan GPS relocation data collected at time intervals different from the survey intervals.

2.5. Model validation

We validated predictions of the reduced model with an independent dataset of GPS locations at hourly intervals from six radio-collared khulan (3 males, 3 females; Fig. A.1).

Animals were marked in mid-summer 2009 and collars collected 1536 relocations (28 July – 29 September) during the period overlapping our 2009 model prediction layers. The data confirmed the extremely high mobility of khulan (Fig. A.1) documented previously (Kaczensky et al., 2008).

The khulan radio-collar locations occurred during four MODIS NDVI 16-day composite periods (see Table 2 in Results). By applying the reduced model, we predicted the probability of the khulan's occurrence for each of the four NDVI periods. From these surfaces we calculated the mean of all pixel values where actual khulan relocations occurred (see Fig. 2 in Results). To test whether this mean was significantly higher than expected by chance, we used random toroidal shifts (splancs library in R) (Rowlingson and Diggle, 1993) to offset the actual relocation patterns 1000 times within a rectangular bounding box which covers the entire study area and encompasses all relocations of khulan. For each random shift of the relocation pattern, we extracted the pixel values of the prediction map and calculated their mean. To determine the significance of our model, we compared 95% quantiles of mean probability of khulan occurrence for the shifted patterns to the mean of the probability of occurrence for the actual relocations of khulan. If the mean of actual relocations is above the 95% quantile of the average probability of the simulated data, this means that the

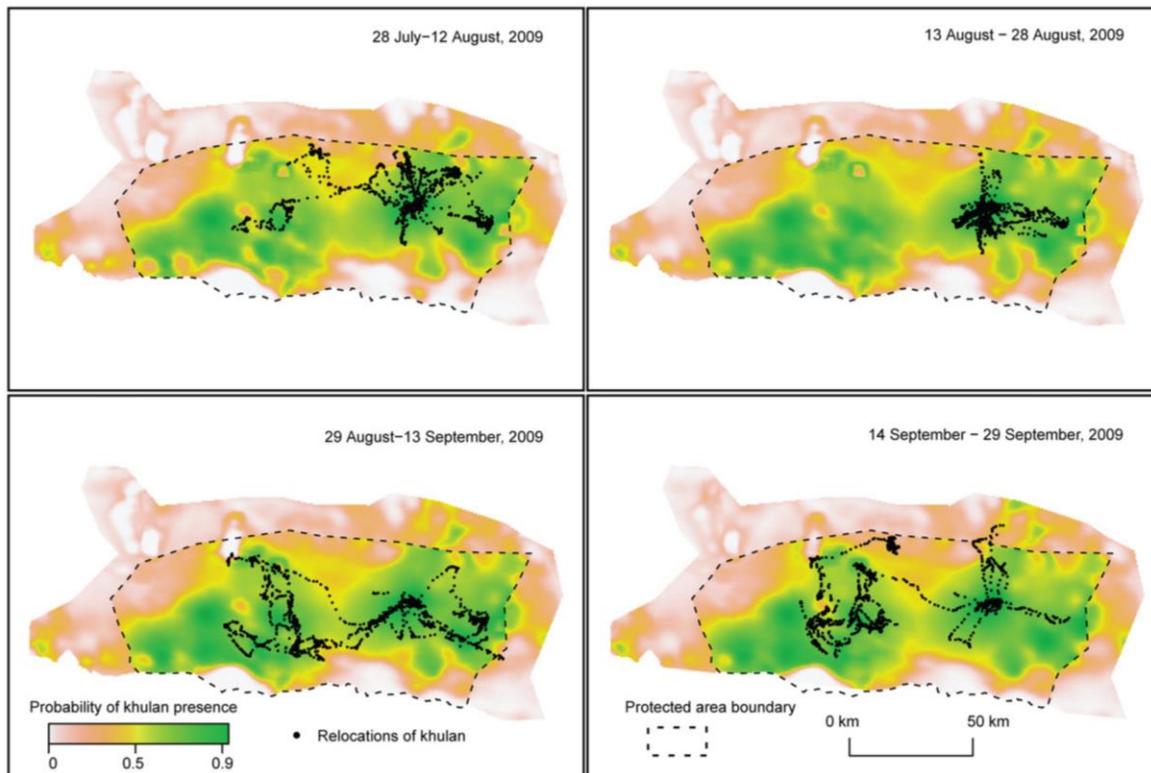


Fig. 2. Predicted probability maps of khulan occurrence (based on the models from the transect data) together with independently collected movement relocation data across four 16-day NDVI intervals in summer 2009. Black dots indicate movement relocations of khulan that correspond to a particular NDVI period. Note that the high degree of mobility of khulan within and between each 16-days interval. Each image contains 2304 relocations of six khulan sampled at hourly intervals.

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model predicted khulan occurrence better than by chance, as the probability that the pattern could have emerged by chance is <0.05 .

2.6. Predictions of habitat dynamics

To assess khulan habitat dynamics for all summer vegetation periods over our six year study period, we acquired the 7 MODIS NDVI 16-day composites for each summer and year and applied the reduced model. We thus generated a total of 42 maps that showed a prediction of khulan occurrence for each NDVI period in each year (Fig. B.1). We then calculated the average and standard deviation across all prediction surfaces. The resulting maps allowed us to assess the degree of dynamics of summer foraging habitat within and among years.

3. Results

The logistic mixed model identified NDVI, elevation, distance to water, and protected area status as significant variables predicting the probability of khulan occurrence (Table 1). Slope was the only variable which was not significant in the model. NDVI and elevation were significant with their second-order polynomials, meaning that intermediate ranges of NDVI and elevation were preferred by khulan (Table 1). The coefficient for distance to water was negative indicating that khulan avoided distances too far from water. The model predicted that for median NDVI, elevation, and inside the protected area, khulan on average tended to stay within 21 km of water sources (Fig. B.2). In addition, our model suggested that there was a higher probability of khulan occurrence inside the protected area than in the buffer zone, and that khulan presence was positively related to goitered gazelle presence (Table 1).

We applied a reduced model using only the habitat covariates, and excluding the autocovariate and the length of survey track to predict khulan habitat (Table 1). The reduced model correctly predicted 74% (257 of 347) of the presence and 48% (166 of 347) of the absence blocks assuming 0.5 probability thresholds. The permutation test with independent movement data showed that in each of the four 16-day NDVI periods the actual relocations had a higher predicted probability of occurrence than the 95% quantile of the random shifts, and thus

demonstrated that our model predicted khulan significantly better than expected by chance (Table 2, Fig. 2).

Based on visual inspection of our 42 prediction maps we did not find significant spatiotemporal variability of summer foraging habitat between or within years (Fig. B.3 and Fig. B.4). The prediction maps showed a consistent pattern and we subsequently calculated a mean prediction map over the entire 6 years. The overall prediction map showed two large and more or less contiguous areas with a high probability of khulan occurrence which meet in the middle of the protected area and some areas of lower probability of khulan occurrence along the fringes in south and north-north-west (Fig. 3). Furthermore, the areas within the buffer zone have a much lower probability of khulan use than areas within the protected area (Fig. 3). A map of the standard deviation of our predictions showed that the main variability in the prediction surface was associated with water sources around larger oasis complexes and the foothills of the high mountains in the southwest (Fig. 4); this was the case both within and among years (Fig. B.5 and Fig. B.6). We examined the independent movement data in relation to these water sources and found that each khulan in average visited 10 (ranging between 5 and 13) different water sources during the summer season. These water sources were in average located 42 km apart from each other (ranging between 1.6 and 100 km, see Fig. A.1).

4. Discussion

4.1. Spatiotemporal dynamics of foraging habitat

We examined dynamics of foraging habitat of khulan in the Dzungarian Gobi during the summer vegetation period. We found that NDVI, elevation, distance to water, and protected area status, were all significant variables in predicting khulan occurrence. Based on NDVI, the only dynamic habitat variable in our model, our analysis showed that khulan selected for areas with intermediate values of NDVI, which helped to delineate the habitats where khulan occurred through the survey periods. Foraging resources were available rather continuously over two large regions within the protected area (Fig. 3). However, these habitats with intermediate values of NDVI did not vary at broad scales and thus prediction maps showed little variation and did not reveal spatiotemporal dynamics in khulan summer foraging habitat. While intermediate NDVI areas helped delineate broad scale foraging habitat and explained the broad regions where khulan occurred, they did not explain why khulan moved such great distances within these regions. This came as a surprise as researchers previously assumed that khulan foraging habitat is highly dynamic and unpredictable in space and time throughout the Gobi desert, and that this unpredictability drives the long-range movement of khulan within the vegetation period (Kaczensky et al., 2011, 2008).

In many other systems and ungulate species, spatiotemporal variability of foraging resources is indeed a main driver for nomadic movements and high mobility. This is especially true for resource-poor regions where animals often have to cope with great variability in the spatiotemporal distribution of ephemeral food resources (Gunn et al., 2008; Hancock et al., 2006; Mueller et al., 2011, 2008). However, our results revealed that khulan summer foraging habitat in the Dzungarian Gobi was rather predictable and showed very little spatiotemporal variability within and between years. In such case, there is little need for khulan to respond rapidly with long distance movements to changing forage resources and track them. This low degree of variation in khulan summer foraging habitat might be related to the fact that the vegetation in the Dzungarian Gobi consists in large parts of shrubland (a mix of small shrubs, forbs and grasses), whereas other studies that found greater variability in foraging habitat were primarily conducted in areas of herbaceous grassland (grasses and forbs) (Mueller et al., 2008; Singh et al., 2010a).

Dynamics of herbaceous and shrub vegetation in drylands are distinct due to different responses of these plants to precipitation in

Table 1
Logistic models predicting khulan presence in the Dzungarian Gobi during the vegetation period (June–September). Null deviance: 900.2 on 691 df; significance code: *, 0.05, **, 0.01, ***, 0.001. (a) Fixed effects of the full logistic mixed model, including a spatial autocovariate, a covariate for the presence of goitered gazelle, and the length of the transect track within each block; residual deviance: 771.4 on 681 df; AIC: 797.4. (b) Fixed effects for the reduced model that was used to create prediction maps excluding covariates for presence of goitered gazelle, auto-covariate and length of survey tracks; residual deviance: 848.59 on 686df; AIC: 864.59.

	Covariates	Estimate	SE	Z	
(a) Full model	(Intercept)	-1.70	0.43	-3.87***	
	Dynamic covariate	NDVI	4.26	1.24	3.34***
		NDVI ²	-4.28	1.26	-3.37***
		Log10 distance to water	-0.67	0.14	-4.54***
	Static covariate	Elevation	6.17	2.02	3.05**
		Elevation ²	-6.34	2.04	-3.10**
		Slope	-0.05	0.15	-0.36
		Boundary	1.26	0.44	2.86**
		Presence of gazelle	0.97	0.20	4.67***
	Accounting covariate	Autocovariate	0.56	0.11	4.78***
		Length of transect	0.02	0.11	0.18
		(Intercept)	-30.52	5.90	-5.17***
	(b) Reduced model	Dynamic covariate	NDVI	23.91	6.08
NDVI ²			-11.85	2.99	-3.95***
Static covariate		Log10 distance to water	-1.72	0.32	-5.23***
		Elevation	32.61	7.83	4.16***
		Elevation ²	-10.55	2.61	-4.03***
		Slope	-0.16	0.10	-1.59
		Boundary	1.03	0.31	3.31***

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Table 2

Comparison of predicted probability of occurrence between random shifts and actual khulan locations to validate the model. Actual movement data consisted of GPS relocations of six collared khulan (N = 1536 for each individual) across four 16-day NDVI intervals in summer 2009. Mean of 1000 random shifts of actual relocation patterns on prediction maps and its 95% quantile compared with the mean of actual relocations of khulan across four NDVI images. Note that in each of the four periods the mean of the probability of khulan occurrence from the actual relocations of khulan is higher than 95% quantiles of the random shifts.

16-day NDVI period	Mean of 1000 shifts	95% quantile of shifts	Mean of actual movement data
28 July–12 August, 2009	0.34	0.54	0.55
13 August–28 August, 2009	0.35	0.64	0.66
29 August–13 September, 2009	0.373	0.57	0.63
14 September–29 September, 2009	0.36	0.553	0.60

terms of growth and water-use patterns (Moreno-de las Heras et al., 2015). Herbaceous vegetation typically shows quick and intense growth pulses within a short term of rainfall and vegetation greenness is dynamic within a season. Conversely plant biomass and green-up phenology for shrub-dominated landscape are associated with longer-term precipitation patterns and vegetation greenness generally varies less over time (Moreno-de las Heras et al., 2015).

Studies conducted in herbaceous grasslands have previously found preference of herbivores for intermediate NDVI and have typically linked it to the forage maturation hypothesis, which predicts herbivores select an intermediate forage biomass to maximize net daily energy intake and is broadly referred to as a trade-off between forage quality and quantity (Hebblewhite et al., 2008; Mueller et al., 2008; Singh et al., 2010a, 2010b). In herbaceous grassland, variation in NDVI can be linked to different growth stages of the same vegetation types, and an intermediate range simply indicates a growth stage with the best trade-off between forage quantity and quality. In addition, most studies that found a preference for intermediate NDVI values (Hebblewhite et al., 2008; Mueller et al., 2008; Singh et al., 2010a, 2010b) have not only been conducted in herbaceous grasslands but also dealt with bovids, ruminants which tend to select for high forage quality rather than quantity. In contrast, the Dzungarian Gobi is shrub dominated and khulan are equids, non-ruminant hind-gut fermenters adapted to process large quantities of low quality forage (Duncan et al., 1990). Because in shrublands variation in NDVI is less related to growth stages, khulan preference for the intermediate NDVI values may be indicative of preferred habitat types, rather than be supportive of the forage maturation hypothesis. Vegetation communities with lower NDVI values are less suitable because they likely feature shrubs interspersed with barren ground and thus offer limited forage. Vegetation communities with

higher NDVI values are likely associated with riparian vegetation. Such riparian areas may be avoided as they are associated with a greater risk of predation and higher rates of insect harassment (Feh et al., 2001).

4.2. Water sources as alternative drivers of long-range movements

Our results suggest a rather predictable and contiguous foraging habitat for khulan in the Dzungarian Gobi. Consequently, the question remains why khulan exhibit long-range movements during summer. Previous studies have shown that equids are dependent on more or less daily access to water during summer, and that distance from water is an essential factor in habitat selection by wild equids (Giotto et al., 2015; Zhang et al., 2015). Our model showed that khulan avoided locations that were further than 21 km from water, and our prediction maps identified some variability at relatively small, localized spatial scales related to the location of water sources (Fig. 4). Thus, it may be the sparsely distributed and spatially patchy water sources which drive the long-range movements of khulan in the Dzungarian Gobi. Similar pattern have been found in African savannah elephants (*Loxodonta africana*) in Namibia's semi-arid system where mobility was induced by switching of water sources in order to access new foraging areas (Polansky et al., 2015). In the context of our study, khulan seem to be able use foraging areas up to a maximum of about 21 km of water sources, after which they are forced to either return to the previously visited water source or continue to a different one. The limited number of and large distance between water sources (e.g. no water source at all in the central part of the study area) thus modulate khulan use of the large contiguous foraging habitat. This was confirmed by our independent movement data that showed that each khulan indeed used many

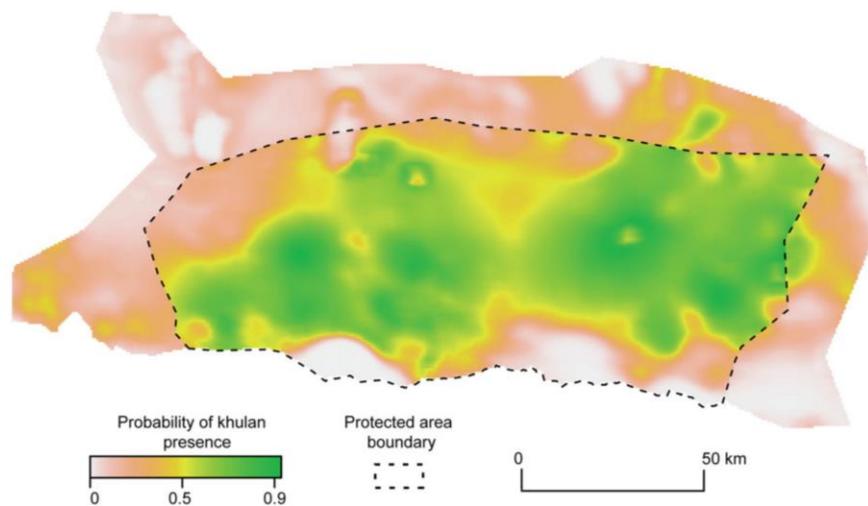


Fig. 3. Mean of 42 predicted probability maps of khulan presence during the vegetation period in the Dzungarian Gobi. Note that the probability of khulan presence in the protected area is generally higher than in the buffer zone area. See Fig. B.3–4 for mean prediction maps within and between years.

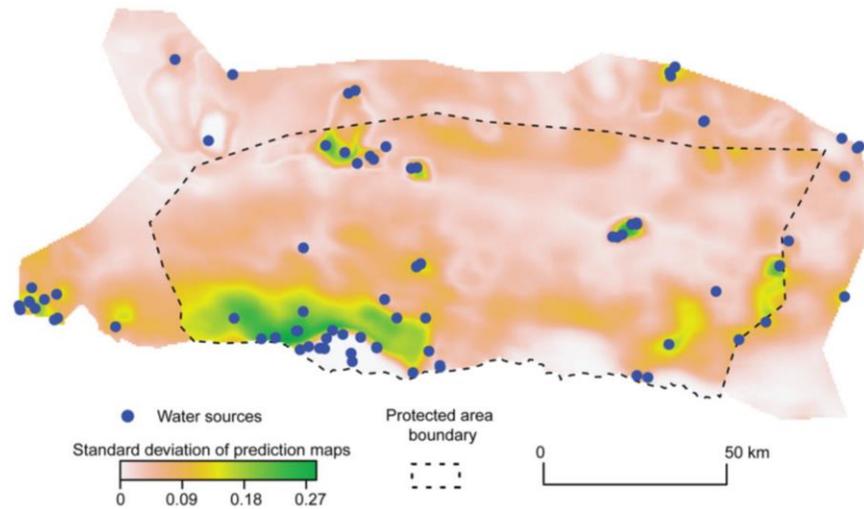


Fig. 4. Standard deviation of the 42 prediction maps of khulan presence and location of water sources. See Fig. B.5–6 for standard deviation maps within and between years.

different water sources that were located up to 100 km apart from each other.

Several explanations why khulan may have to switch between water sources are possible and may be inter-related. Since the areas around water sources were the most prone to habitat variability during summer periods, the attraction of different water sources to khulan can be expected to vary as well. Khulan preference may also be influenced by changes in water quality (e.g. salinity, contamination with animal urine and feces), micro-climate (e.g. wind which holds biting insects at bay), and presence or absence of other species (Zhang et al., 2015), including predators (Péruquet et al., 2010; Valeix et al., 2009). In addition, vegetation adjacent to water sources that varies considerably with the water level and leads to the variability in NDVI may provide small scale but nevertheless valuable foraging. Variability of these small scale vegetation areas may be an additional driver for the long distance khulan movements. Disentangling these factors will be essential for fully understanding the long distance movements of khulan.

4.3. Non-habitat effects on khulan occurrence

In addition to the environmental habitat variables, we also found other effects on khulan occurrence such as protected area status and the presence of goitered gazelle. The probability of khulan occurrence was higher inside the protected area as compared to the buffer zone. This could be an effect of better protection of khulan against illegal hunting inside the protected area due to ranger presence, or a reaction to khulan preferring areas without herder camps and livestock presence as suggested previously for khulan and other ungulates in Mongolia (Kaczensky et al., 2011; Olson et al., 2011; Young et al., 2011). However, in the Dzungarian Gobi, herders and their livestock tend to leave the hot plains in summer and move into the foothills and mountains north of the protected area (von Wehrden et al., 2006).

Our results indicate that current protected area management is having a positive effect on khulan presence in the area. Therefore, strictly regulating livestock presence and controlling human activity within the protected area should remain a key focus of ranger patrols. Moreover, the occurrence of goitered gazelle was positively correlated with the occurrence of khulan. Unfortunately, detailed research on interactions between khulan and goitered gazelle does not exist. However, in other systems, mutual interactions with regard to feeding facilitation or predator avoidance among large mammalian herbivores has been

documented (Sinclair and Norton-Griffiths, 1982) and may also be relevant in the Gobi.

5. Conservation implications

Recent studies in movement ecology suggest that long-ranging species are increasingly threatened as a consequence of human land-use and climate change (Hobbs et al., 2008; Luo et al., 2015). Therefore, scientists have been focusing on understanding patterns and drivers of population-level long-distance movement and linking it with large-scale conservation efforts that attempt to maintain habitat connectivity for highly mobile species (Allen and Singh, 2016). Conservation management based on predictable animal movements, both migration and residence, is possible as we can anticipate connectivity among suitable habitats and resources and maintain ecological corridors between fragmented habitats. However, if a species has unpredictable movements or is nomadic it is more difficult to assess where ecological corridors need to be placed (Runge et al., 2014). Understanding which component of abiotic environmental variability is most important for promoting nomadic movement and how animals cope with resource dynamics and changing conditions is essential in order to identify the scale of conservation management and to develop a long-term conservation strategy for these species.

One key management implication of our study relates to the finding that long-range nomadic movements of large herbivores in resource poor landscapes are not always directly coupled with highly variable and unpredictable vegetation productivity. In the Dzungarian Gobi, sparsely distributed and patchy water sources, rather than dynamics of foraging habitats, appears to be the driver for long distance nomadic movement of khulan in summer. Our findings thus highlight that access to patchy key resources like water and connectivity among water bodies are critical for water-dependent grazers and nomadic species in arid and semi-arid, resource-poor landscapes. We are still only at the beginning of our understanding of what possible drivers under which circumstances drive nomadic, long-range movements in ungulates. Only a sound understanding of landscape scale drivers of long-range movements in khulan and other nomadic ungulates will allow us to minimize, mitigate, or offset the potential adverse effects of ongoing and future infrastructure development in drylands. Since khulan occurred more frequently inside than outside the protected area, this study also highlights successful landscape-scale conservation of the protected area that has been conserving wildlife since 1975. It encompasses many sparsely

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distributed water sources from smaller springs to large oases. However, throughout the expanse of the entire Gobi in Mongolia, only about 27% of the khulan range are covered by protected areas (Buuveibaatar et al., 2016a) and future studies are needed to understand what makes khulan and other water-dependent wildlife choose certain water points and how wildlife use is influenced by environmental or anthropogenic factors throughout the expanse of the entire Gobi. Overall, conservation efforts to maintain nomadic herbivores should focus on functional connectivity among forage and other key resources such as water bodies and their extent. Future studies outside protected areas should focus on routing and frequency of animal movements among water bodies to provide deeper insights into where and how conservation measures could improve functional connectivity among resources.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.biocon.2016.10.021.

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APPENDICES: A.1 Spatiotemporal habitat dynamics of ungulates in unpredictable environments: The khulan (*Equus hemionus*) in the Mongolian Gobi desert as a case study

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Supplementary material for A.3

Appendix A: Description of datasets which are used for the model building (Table A.1 and Table A.2) and the model validation (Figure A.1).

Appendix B: Prediction maps of probability of khulan presence between 2004 and 2009 and their variability within and between years – Figure B.1-B.6.

Appendix A

Table A.1. Survey dates, matching NDVI images (16-day intervals) and distances of survey tracks.

Year	Survey date		NDVI image date		Survey distance, km
	Start	End	Start	End	
2004	08-08	08-12	07-27	08-11	800
2005	06-09	06-13	06-10	06-25	789
2005	08-20	08-24	08-13	08-28	856
2006	06-16	06-18	06-09	06-24	782
2006	08-12	08-14	07-27	08-11	783
2007	06-17	06-21	06-10	06-25	877
2008	06-11	06-13	06-09	06-24	754
2008	08-15	08-18	08-12	08-27	745
2009	06-11	06-13	06-10	06-25	714
2009	07-28	07-30	07-12	07-27	750
2009	08-06	08-08	07-28	08-12	768
2009	09-11	09-14	08-28	09-12	725

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Table A.2. Data for survey and 5 km² blocks which we used for analysis in the Dzungarian Gobi in Mongolia between 2004 and 2009.

Survey ID year-month	Survey data				Data within 5 km ² blocks				Presence data	
	Groups		Abundance		Groups		Abundance		within 5 km ² blocks	
	khulan	gazelle	khulan	gazelle	khulan	gazelle	khulan	gazelle	khulan	gazelle
2004 8	68	78	849	327	67	43	839	166	38	24
2005 6	126	102	3754	297	126	78	3754	250	52	45
2005 8	54	79	765	544	54	38	765	256	26	18
2006 6	173	182	1567	479	170	120	1504	280	53	46
2006 8	60	98	1909	499	58	39	1893	236	33	20
2007 6	53	97	2466	394	51	58	2367	269	28	24
2008 6	29	71	487	266	29	22	487	67	17	15
2008 8	39	66	4096	426	36	28	3997	222	18	14
2009 6	33	69	898	240	32	33	892	128	19	20
2009 7	27	133	463	694	27	54	463	326	19	25
2009 8	33	86	4577	682	33	43	4577	320	24	20
2009 9	28	75	1063	539	27	20	1061	166	20	13
Total	723	1136	22894	5387	710	576	22599	2686	347	284

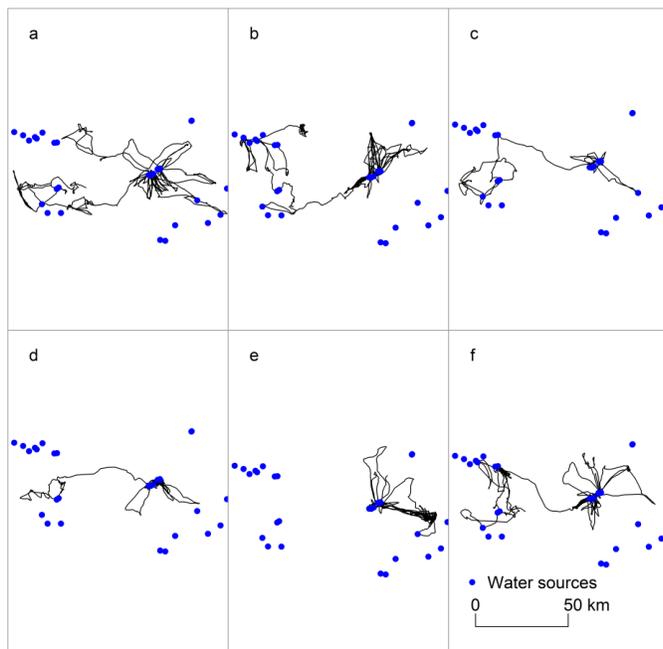


Figure A.1. Long-range movement paths of six khulan during the vegetation period. Each panel (a-f) shows a path of a single khulan based on hourly relocations between 28th July and 29th September in 2009. Each khulan in average visited 10 (ranging between 5 and 13) different water

sources during the summer season. These water sources were in average located 42 km apart from each other (ranging between 1.6 and 100 km).

Appendix B



Figure B.1. Prediction surfaces of seven 16-day NDVI periods across six years (2004-2009).

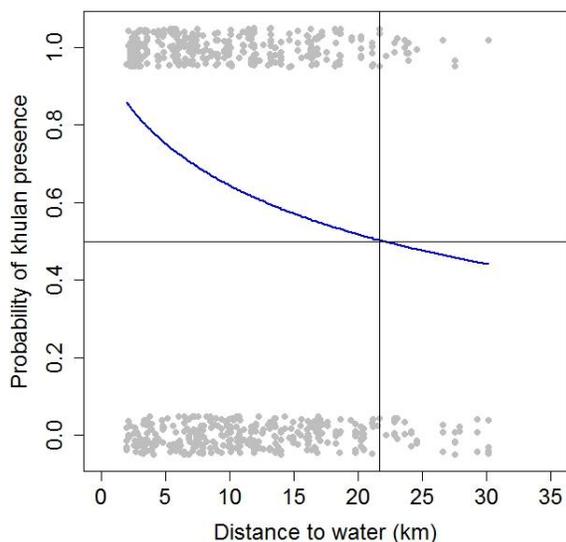


Figure B.2. The relationship between probability of khulan presence and distance to water based on the reduced model in Table 1. For prediction we assumed median NDVI, elevation, and slope and a location inside the protected area, khulan probability of occurrences was above 0.5 within 21 km of water sources.

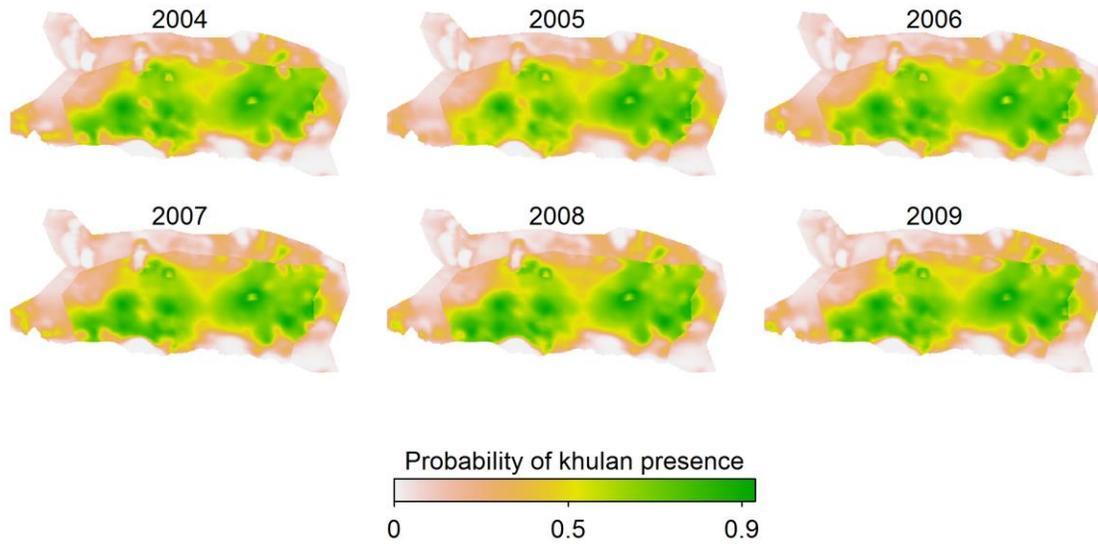


Figure B.3. Mean of seven prediction surfaces of the 16-day NDVI periods during summer within each year (2004-2009). Foraging habitats of khulan show little variability within summer periods.

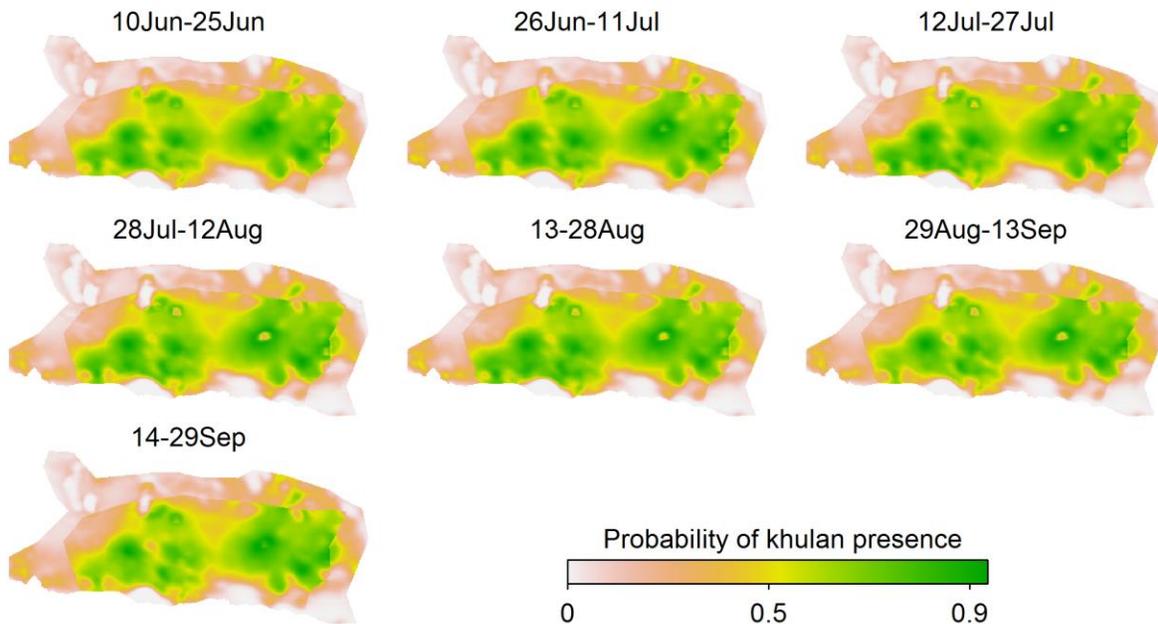


Figure B.4. Mean of six prediction surfaces of each 16-day NDVI period across years (2004-2009).

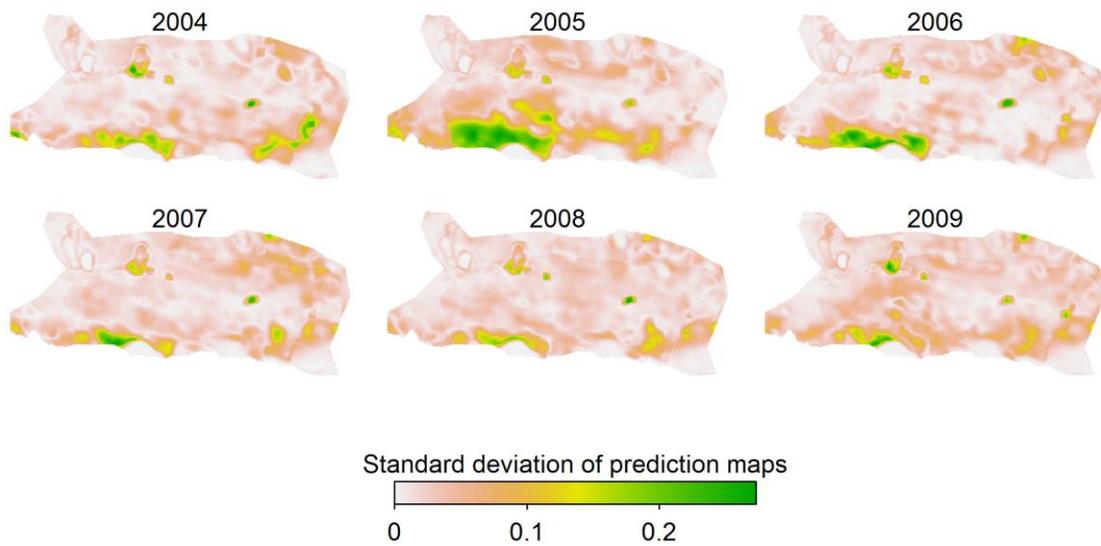


Figure B.5. Standard deviation of seven prediction surfaces of the 16-day NDVI periods during summer within each year (2004-2009).

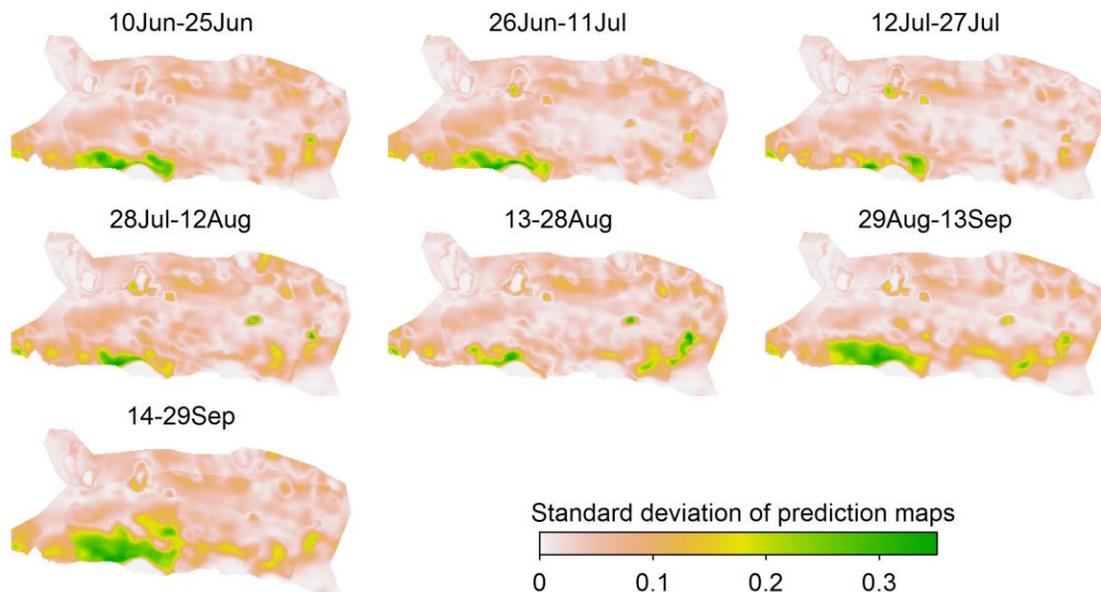


Figure B.6. Standard deviation of six prediction surfaces of each 16-day NDVI period across years (2004-2009).

A.2 Challenges in the conservation of wide-ranging nomadic species

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Challenges in the conservation of wide-ranging nomadic species

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Abstract

1. Conservation of nomadic species presents significant conservation challenges because of unpredictability in their movements and space use. Long-term studies on nomadic species offering insights into the variability in space use within and between years are largely missing but are necessary to develop effective conservation strategies.
2. We examined the temporal variability in space-use of Mongolian gazelle, a nomadic species. We tracked 22 individuals for 1–3 years with GPS and used the resulting movement patterns to evaluate conservation strategies associated with their nomadic movements in the intact open plain grasslands of Mongolia. Individuals exhibited a high degree of variability in space use within and between years, often using different wintering areas in different years. The individual range size varied as much as threefold between years, with an estimated average annual individual range size of ~19,000 km² and a lifetime range of ~100,000 km².
3. Comparing simulated and empirical GPS trajectories for the Mongolian gazelle showed that they avoided disturbed areas (e.g. oil fields) and did not prefer protected areas. Importantly, no single protected area in the region was large enough to cover the annual range of any of the tracked gazelle.
4. Because of their wide-ranging movements, the presence of linear infrastructure and the resulting barrier effects are a particular concern. We found that fences along the national border were absolute barriers affecting movements of about 80% of all tracked individuals. When gazelle encounter the border fence, they moved a median distance of 11 km along fences, suggesting frequent crossing options are needed to make barriers permeable.

5. *Synthesis and applications.* We show that for nomadic species whose space use varies greatly across years, multiyear movement data are essential for sound conservation planning. We emphasize that place-based approaches alone are insufficient to conserve wide-ranging nomadic species and that linear infrastructure, including fences, highways and railroads, is of particular concern. Because nomadic species lack defined movement corridors, we advocate integrated land use planning that prioritizes permeability across the entire landscape and facilitates long-distance movements. We suggest that conservation strategies for nomadic species in arid and semi-arid regions be reconsidered based on multiyear connectivity assessments at the landscape scale.

KEY WORDS

animal movement, crossing structure, land use, nomadic, permeability, protected area, ungulate, wide-ranging species

1 | INTRODUCTION

Integrating animal movements into conservation management is critical to conservation success (Allen & Singh, 2016; MCGOWAN ET AL., 2017). Conservation challenges are magnified for highly mobile species that have large ranges and high spatiotemporal variability in space use. Spatiotemporal variability and its potential implications for conservation management remain understudied, in large part due to a lack of suitable datasets (Kays, Crofoot, Jetz, & Wikelski, 2015; Runge, Martin, Possingham, Willis, & Fuller, 2014).

Consideration of movement strategies, such as range residency and migration, is crucial to protecting wildlife. For example, conservation of long-distance migrants with predictable migration routes can be facilitated through corridors that maintain connectivity between seasonal habitats (Sawyer, Kauffman, Nielson, & Horne, 2009). In other cases, management efforts focus on protecting areas that are regularly used during key parts of the species' life cycle (e.g. breeding and wintering areas; Geldmann et al., 2013).

While migratory and range resident species are well studied, few studies address nomadic species, and even fewer consider conservation planning for them (Runge et al., 2014). Nomadic species, like Thomson's gazelle *Eudorcas thomsonii* in the Serengeti Plains or khulan *Equus hemionus* in the Gobi Desert, are typically found in resource-poor, arid environments with dynamic resources (McNaughton, 1976; Nandintsetseg, Kaczensky, Ganbaatar, Leimgruber, & Mueller, 2016). The key characteristics of nomadic movements are non-seasonal spatial variability and temporal unpredictability in interannual space use (Jonzén & Knudsen, 2011). However, few studies on nomadic species examine the predictability of space use by multiple individuals monitored over more than 1 year, which is key information for their long-term survival. Studies on the use of protected areas (PAs) or the effects of disturbance on nomadic species are likewise scarce.

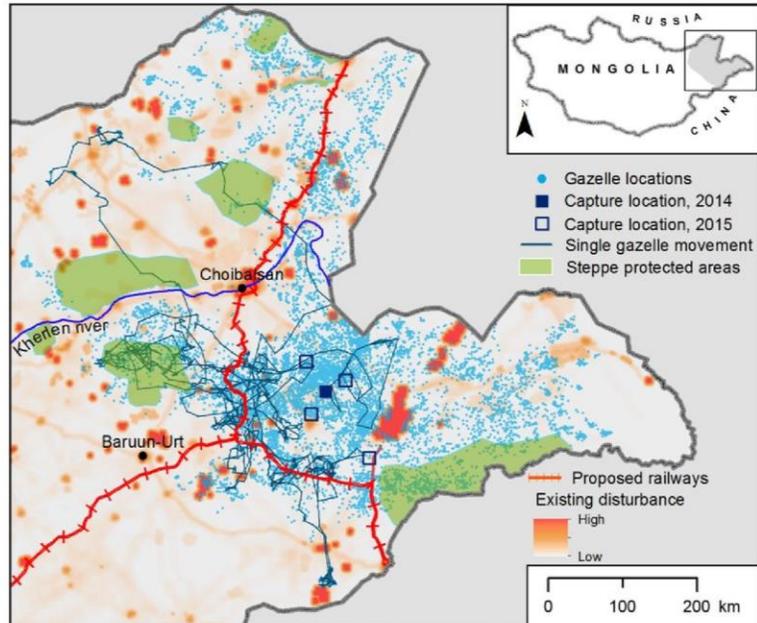
Here, we study the Mongolian gazelle *Procapra gutturosa* (hereafter gazelle), a prominent example of a nomadic ungulate (Mueller et al., 2008; Olson et al., 2010) and one of the most numerous gazelle

species globally. They are native to the open steppe of Mongolia and the adjacent areas of Russia and China (Mallon, 2008). Over 95% of the global population of gazelle occurs in Mongolia's steppe. Based on a 2002 estimated population size of 1 million gazelle (Olson et al., 2010), the species is listed as Least Concern in the IUCN Red List (Mallon, 2008). Although the population trend is assessed as stable in the IUCN Red List, there has been no regional scale population census since 2002, and thus the population trend is unknown. The population does undergo substantial fluctuations in abundance due to overhunting, disease outbreaks and extreme weather events, and gazelle are considered as endangered in Mongolia's Red List (Clark et al. 2006).

Gazelle undertake long-distance movements driven by high inter- and intraannual variability in resource availability in the steppe (Mueller et al., 2008). Observed group sizes range from a single individual to more than 200,000 individuals (Olson, Mueller, Bolortsetseg, et al., 2009). An individual gazelle can roam over 32,000 km² in 1 year (Olson et al., 2010). The species' core distribution range in eastern Mongolia is 200,000 km² ± 3,100 km² (Fleming et al., 2014). Apart from attention given to annual range sizes, relatively little is known about the lifetime space requirements or the predictability of areas used by individual gazelle, particularly at critical stages of their life cycle (e.g. calving and wintering periods).

A mosaic of PAs was established in part to safeguard remaining gazelle populations in eastern Mongolia, which are threatened by poaching, competition with livestock, and habitat loss and fragmentation (Olson & Fuller, 2017; Figure 1). These unfenced PAs often have a habitat characteristics similar to their immediate vicinity. Fences alongside the Trans-Mongolian Railway and Mongolia's national border are proven barriers for gazelle, further fragmenting their habitat outside the species' core range (Ito et al., 2008). Furthermore, the rapidly growing extractive industry in Mongolia has led to proposals to construct new railways. Mongolia has a state policy on railway transportation (Parliament resolution no. 32 in 2010), which plans the construction of 5,683.5 km of new railways (Gansukh, Ming, &

FIGURE 1 Mongolian gazelle GPS locations with existing and proposed disturbances and protected areas in the core range of Mongolian gazelle in Mongolia



Ali, 2018) and road corridors across the core ranges of several ungulates, including gazelle (Figure 1). These emerging developments will increase habitat fragmentation and likely result in additional movement barriers to gazelle movements (Batsaikhan et al., 2014).

Here, we used multiple-year GPS movement data of gazelle in the Eastern Steppe to examine spatiotemporal variability in space use relative to conservation measures for gazelle. First, we measured the variability in space use among individuals in the same year and within individuals between years. Second, we evaluated current conservation measures for gazelle by examining the use of the PAs and by assessing the effects of anthropogenic disturbance on gazelle movements. Lastly, we assessed the effect of linear infrastructure on gazelle movements and provide recommendations for the future conservation of gazelle, which can be relevant for other wide-ranging nomadic species in arid and semi-arid regions.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was conducted in the Eastern Steppe of Mongolia, one of the largest temperate grasslands in the world (Figure 1; Carbutt, Henwood, & Gilfedder, 2017). The steppe features broad plains and rolling hills dominated by grasses. Precipitation (~200 mm annually) can be highly variable across space and time resulting in high variability in vegetation productivity (Vandandorj, Gantsetseg, & Boldgiv, 2015). Land use policy favours communal use by traditional livestock pastoralists, although other land use occurs (e.g. agriculture, settlements, mining).

2.2 | Empirical movement data

We used data from 22 gazelle (12 collared in October 2014, Sample 1; 10 in September 2015, Sample 2) which were monitored for 1–3 years, providing a total of 12,166 daily GPS positions (Figure 1, details in Table S1 and an animation of the movements in Animation S1). Although our dataset is limited to 22 individuals, it currently constitutes the largest long-term dataset of gazelle (Nandintsetseg et al., 2019).

2.3 | Simulated movement model

We used simulated random movement paths as a null model to assess three objectives: (a) the predictability of space use between years, (b) the use of PAs and (c) the effect of disturbance on gazelle space use. We generated correlated random walks by drawing step lengths and turning angles from the empirical distributions of each GPS tracked gazelle. We drew daily steps for each individual's tracking period. We simulated gaps in these random paths by removing positions from the full simulated trajectories corresponding to the gaps in the empirical movement paths. This resulted in simulated paths that had the same number of positions as the empirical paths. We bounded simulated paths by the Mongolian border and the Trans-Mongolian Railway fences that restrict gazelle movements. We simulated 1,000 replicate paths for each individual. For further details, see Description S1.

2.4 | Range estimation and temporal variability in space use

To examine variability in annual space use of gazelle among individuals and across years, we used minimum convex polygons as a metric

of annual space use per individual (95% MCP, `maptool` R package; Calenge, 2017). We used MCP because it can be compared to previous studies and data densities across individuals were similar. We calculated annual ranges for each gazelle, resulting in a total of 40 annual ranges. Not all gazelle survived the full 3 years; there were 22, 13 and 5 individuals with 1, 2 and 3 years of tracking data respectively (Table S1).

We used Autocorrelated Kernel Density Estimation (AKDE, `ctmm` 0.4.1 R package), a novel home range estimator that allows the use of autocorrelated movement data, to reliably estimate lifetime ranges as described in Fleming et al. (2015). Lifetime range refers to predictions of range use beyond the tracking period, assuming that the movement behaviour stays constant (Calabrese, Fleming, & Gurarie, 2016; Fleming et al., 2015). We could not estimate the lifetime ranges using AKDE for 10 individuals (those tracked for a single year) because the semi-variance (i.e. the average square displacement vs. time-lag) did not approach an asymptote with increasing time-lags, that is they likely had not been tracked long enough to allow for accurate estimates.

In addition, we examined the predictability of an individual's space use. We specifically were interested in how the predictability in space use varied between wintering and calving periods. We evaluated this variability for 12 female gazelle by calculating the pairwise distances between centroids of a sequence of 14-day intervals throughout the year, thus comparing the same time of year between years for each gazelle with at least 2 years of data. We used a paired *t* test to compare average pairwise distances between calving and wintering periods for each individual. Due to synchronized and short birthing and nursing periods (Olson, Fuller, Schaller, Lhagvasuren, & Odonkhuu, 2005), we defined the calving period as the time spanning 25 June until 23 July. To match the number of days for calving and wintering periods, we also selected three 14-day intervals in the middle of winter and defined the wintering period as 8 January to 5 February. To compare the wintering and calving mean pairwise distances of the tagged gazelle to the null model, we also calculated the pairwise distance in the same way for each simulated individual trajectory. We then estimated the *p*-value with a randomization test to determine if the mean pairwise distances of tagged gazelle during wintering and calving periods were significantly different than the null distributions based on the simulated paths (Figure S3).

2.5 | Assessing use of PAs and effects of disturbance on space use

We evaluated the gazelle' use of PAs by comparing the proportion of daily GPS positions inside PAs for each gazelle (i.e. the ratio of the number of gazelle daily GPS positions inside the PAs to the total number of daily GPS positions) to that of the simulated paths. We then used a randomization test to assess whether the median proportion of PA use across all tagged gazelle was significantly greater than the distribution of median PA use by the simulated individuals, under the hypothesis that tagged gazelle use PAs more than the null model.

To measure effects of human-induced disturbances on gazelle movements, we used a cumulative disturbance index layer for the Eastern Steppe (Heiner et al., 2016). This layer was created using five anthropogenic factors, including herder household locations, agricultural use, existing mining areas, population centres, and linear infrastructure such as roads and railways. The disturbance index ranges from 0 (*no disturbance*) to 1 (*high disturbance*). For each gazelle, we extracted the disturbance index pixel values at each position, and used the median across locations to characterize the disturbance experienced by gazelle. We applied the same procedure to the 1,000 simulated gazelle paths for each individual. We then compared the range of medians of the disturbance index for the simulated paths to the median of the disturbance index of the tagged gazelle. Using a randomization test, we assessed whether the median disturbance index across all gazelle was significantly lower than that for simulated paths, under the hypothesis that tagged gazelle use disturbed areas less than the simulation model which has no avoidance behaviour.

2.6 | Effects of linear features on gazelle movements

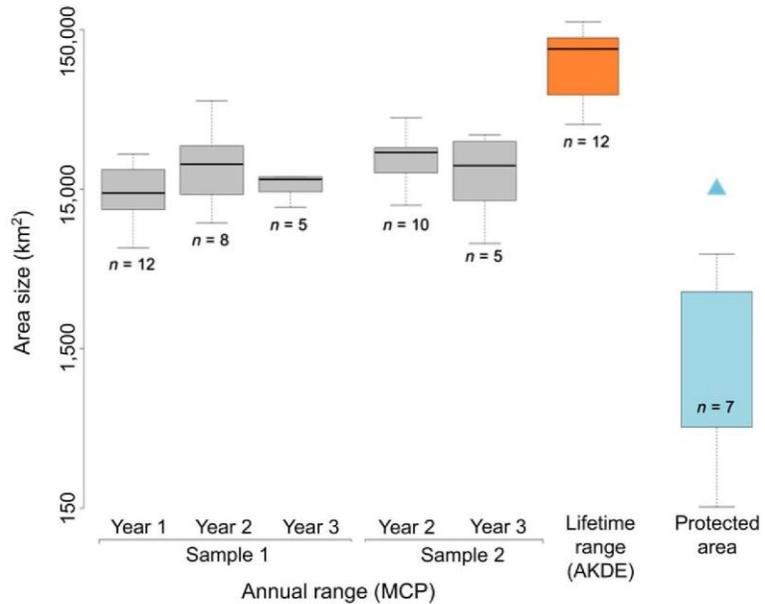
To explore how gazelle react to linear barriers, we examined the effects of the Mongolian border fence on gazelle movements. When gazelle approach the border fence, they frequently travel along it, presumably trying to cross. We calculated the travel distances along the border fence for each encounter with the border. We considered positions within 5 km of the border to be fence encounters and treated all subsequent positions within 10 km of the border fence as part of the same encounter travelling along the border before giving up (Figure 5b). We selected 5 km as the threshold based on visual line of sight distances to the horizon under perfect clarity and flatness (Martínez-García, Calabrese, Mueller, Olson, & López, 2013). We feel this is reasonable because gazelle may be able to use other non-visual cues (e.g. acoustic and social cues) and given our daily sampling, it is possible that the gazelle were closer than 5 km to the border fence between two sampling events. We used a larger giving-up threshold of 10 km to avoid breaking a single encounter into multiple encounters simply because one data point was slightly farther away. To define the travel distances, we first projected each gazelle position in an encounter event to the closest point on the border. For each fence encounter, we then calculated the distance along the border encompassing all the projected points on the border. We also calculated the number of border encounters and number of days gazelle stayed in proximity to the border.

3 | RESULTS

3.1 | Spatiotemporal variability in space use of gazelle

The mean annual range of a single gazelle was 19,346 km² (*n* = 40 annual ranges, Figure 2), but this varied greatly among individuals

FIGURE 2 Annual range (MCP) and lifetime range estimations (AKDE) of individual Mongolian gazelle compared to the sizes of protected areas in the eastern Mongolia on a log scale. Not all individuals survived the entire study period and the sample size decreases with study years for both samples. The boxplot of annual ranges indicate within-year variability and comparison among boxplots indicates between-year variability of ranges. The triangle represents the total area of all seven protected areas



($SD = 9,265 \text{ km}^2$). The largest annual range ($53,422 \text{ km}^2$) of a single gazelle was more than eight times larger than the smallest ($6,431 \text{ km}^2$, Figure 2). Within the same year and the same region, the range size among individuals varied up to six times. Considerable variability in space use also occurred by the same individuals among years. Annual range size varied up to three times for the same individual across years (e.g. from $17,890$ to $53,422 \text{ km}^2$ for one or from $12,696$ to $37,447 \text{ km}^2$ for another individual, Table S1).

The average range size across all gazelle varied less among years: for the 12 females that were all caught in the same location and the same year (Sample 1), range sizes varied from $14,934 \text{ km}^2$ ($n = 12$, $SD = 5,502 \text{ km}^2$) in year 1 to $23,556 \text{ km}^2$ ($n = 8$, $SD = 14,113 \text{ km}^2$) in year 2 and $17,602$ ($n = 5$, $SD = 5,805 \text{ km}^2$) in year three (Sample 1 in Figure 2). Similarly, for the 10 individuals of Sample 2, the average range was $21,500 \text{ km}^2$ ($n = 10$, $SD = 7854$) in year 2 and $20,637 \text{ km}^2$ ($n = 5$, $SD = 7854 \text{ km}^2$) in year 3 (Sample 2 in Figure 2).

Lifetime ranges of individual gazelle estimated with AKDE averaged $100,800 \text{ km}^2$ ($n = 12$, $SD = 45,356 \text{ km}^2$), ranging from $38,100$ to $167,841 \text{ km}^2$. The average range crossing time was 6 months (Figure 2, Table S2). The average lifetime range was six times larger than the total size of the PAs ($15,000 \text{ km}^2$; Figure 2).

The predictability of space use across years based on the 14-day interval pairwise distances showed the mean pairwise distance was 134 km , indicating that in general, gazelle did not visit the same places across years (Figure 3). The mean pairwise distance between calving areas in different years was 91 km ($n = 12$, $SD = 49$), which was significantly lower than distances for the wintering periods ($p = 0.002$, $df = 11$). In contrast, during wintering periods, the mean pairwise distance was 176 km ($n = 12$, $SD = 91$), indicating that individual gazelle sought and utilized wintering areas that were farther apart in different years than the distances between areas occupied

during the calving period (Figure 3). The shorter pairwise distances during calving time indicate that individual gazelle inhabited areas in relative proximity to those which they had used in previous years. When comparing mean pairwise distance during calving to the null model, we found three individuals that had significantly smaller distances than the null model, indicating individual-level variability in spatial predictability during calving periods (Table S3). During winters, pairwise distances for all individuals were not significantly different than the null model (Table S3).

3.2 | Effects of protected and disturbed areas on gazelle space use

Gazelle passed through seven PAs, but they did not use the PAs more than expected by chance (Figure 4a, Animation S1). The median of the proportion of positions inside PAs of tagged versus simulated gazelle was similar, and we did not detect a significant difference (Figure 4a, Animation S1). However, we found a significant difference between the median disturbance index for tagged and simulated gazelle paths, indicating that gazelle avoided disturbed areas (e.g. population centres, extractive industry sites; Figure 4b).

3.3 | Effects of border fences on gazelle movements

About 80% (17 of 22) of the tagged gazelle encountered the border fence at least once during the study period (for a total of 39 fence encounters) even though the original tagging locations were far from the border fence (up to 100 km , Figure 1). Movement behaviours of gazelle were extremely variable when approaching the border fence. On average, gazelle moved along the border fence for 10 days, but

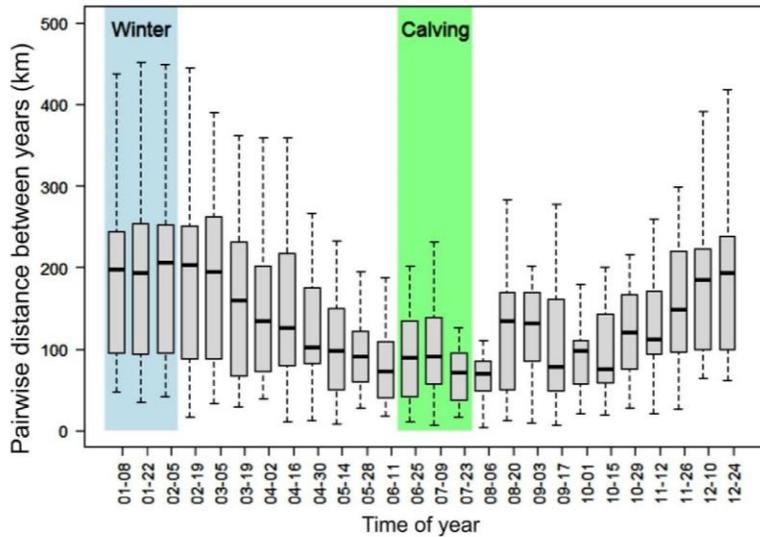


FIGURE 3 Predictability of space use between years. Each boxplot represents the distribution of pairwise distances between two 14-day mean locations of the same individual in different years. Areas used by Mongolian gazelle during wintering periods were more variable than calving periods

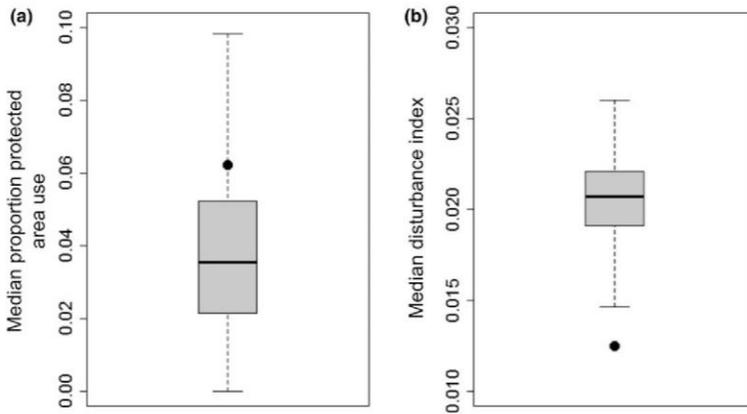


FIGURE 4 (a) A comparison of the median proportion of protected area use by tagged Mongolian gazelle (black circle) with the medians of 1,000 replicate simulations (boxplot) showed that Mongolian gazelle used protected areas similarly to random chance ($p = 0.15$). (b) A comparison of the median disturbance index for the tagged Mongolian gazelle (black circle) with medians from 1,000 replicate simulations showed a strong avoidance of disturbed areas ($p = 0.003$). We estimated the p -value using a randomization test

some gazelle moved along the border for as long as 59 days, and still others turned back within a day. The distance gazelle moved along the border fence ranged from a few hundred meters to 80 km with a median distance of 11 km (Figure 5a).

4 | DISCUSSION

4.1 | Variability of space use in nomadic movements

Variability of individual behaviour, including individual variation in space use, is a key factor in ecology and evolution that should receive greater attention in conservation (Merrick & Koprowski, 2017). This is particularly important for nomadic species that display movement behaviours with large individual differences within and between years.

Our study highlights the importance of long-term monitoring of space use for nomadic species and emphasizes three aspects of the

spatiotemporal dynamics of space use in nomadism: (a) individual differences in space use within and between years; (b) lack of fidelity to particular areas for key stages in the life cycle (e.g. calving, rutting, wintering); and (c) large lifetime ranges.

First, with regard to variability in space use among individuals in the same year, we found that an individual gazelle occupied a large area in a single year, on average $\sim 19,000 \text{ km}^2$ —about the size of Kruger National Park in South Africa. Some gazelle had up to six times larger ranges than others, indicating individual behavioural differences in space use (Figure 2). Moreover, we found gazelle exhibit substantial behavioural flexibility over time with ranges varying by a factor of three from 1 year to the next. Second, this variability was also prevalent in the lack of site fidelity to specific wintering areas, and the average distance between wintering areas in different years was 176 km ($SD = 91 \text{ km}$). The areas used by gazelle during the calving period, on the other hand, showed less variability, but the distance between calving grounds in different years was relatively large

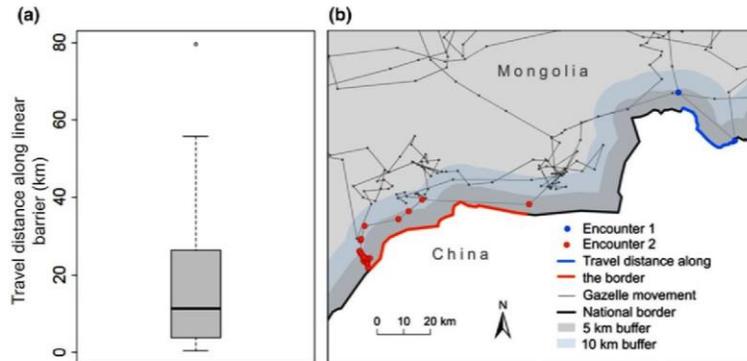


FIGURE 5 The effects of the Mongolian border fence on Mongolian gazelle movements. (a) The distribution of Mongolian gazelle travel distances along the border fence. (b) Illustration of two encounters of a single Mongolian gazelle with the border fence and their travel distances. For encounter 1 (in blue), the Mongolian gazelle left the fence within a day and the travel distance along the border was ~20 km. For encounter 2 (in orange), the Mongolian gazelle was in the proximity of the border for ~20 days and the travel distance was ~50 km

(91 ± 49 km), suggesting little evidence for the existence of ‘calving grounds’ or seasonal ranges referred to in the literature (Gunn & Miller, 1986; Ito, Tsuge, et al., 2013; Leimgruber et al., 2001; Olson et al., 2010).

The between-year variability in space use is likely driven by unpredictable changes in resource availability across the landscape, as has been also shown for other nomadic species in arid environments (Jonzén & Knudsen, 2011; Roshier, Doerr, & Doerr, 2008). In summer, gazelle movements are driven by the patchy distribution of high-quality vegetation due to rainfall variability (Mueller et al., 2008, 2011). In winter, gazelle movements are likely driven by a combination of higher forage availability and shallow snow depth, which are unpredictable in space and time (Ito, Tsuge, et al., 2013; Luo, Liu, Liu, Jiang, & Halbrook, 2014), explaining the lack of fidelity to wintering areas over time. Searching out lower snow depths for easier movement and better access to forage is a widespread behaviour of ungulates in winter (Avgar, Mosser, Brown, & Fryxell, 2013; Gilbert, Hundertmark, Person, Lindberg, & Boyce, 2017; Nicholson, Arthur, Horne, Garton, & Del Vecchio, 2016).

Lastly, we found that individual gazelle have extremely large estimated lifetime ranges. Although the average annual range was $19,346 \text{ km}^2$ (MCP), the estimated average lifetime range for a single gazelle was $100,800 \text{ km}^2$ (AKDE, Figure 2), which is half of the population core range of gazelle (~ $200,000 \text{ km}^2$; Fleming et al., 2014) and is four times larger than the area covered by ~1.2 million wildebeest *Conochoaetus taurinus* during their annual migration through the Serengeti-Mara ecosystem ($25,000 \text{ km}^2$) (Thirgood et al., 2004). The average lifetime range for gazelle is about the same size as the total area used by 54 caribous *Rangifer tarandus granti* over 4 years in the Canadian Northwest Territory ($84,543 \text{ km}^2$; Nicholson et al., 2016). However, we note that these estimates of other ungulates in different systems were not calculated with AKDE and that actual lifetime ranges of gazelle may be somewhat smaller than we estimated here, because AKDE does not take into account barriers.

4.2 | Conservation strategies for nomadic species

Nomadic gazelle's individual variability in space use between years, their large lifetime area needs, and especially their lack of fidelity to wintering and calving areas all highlight the importance of landscape permeability. All the gazelle we tracked had lifetime ranges larger than any of the PAs (Figure 2), and the PAs were only sporadically used by gazelle (Figure 4a, Animation S1), indicating that PAs are not an effective conservation measure for the species. The individual lifetime range of over $100,000 \text{ km}^2$ suggests that the scale of conservation management must go considerably beyond the scale of existing PAs (up to $6,000 \text{ km}^2$). At present, however, PAs are currently the only conservation measure for the gazelle and cover ~8% of the gazelle range in Mongolia.

Studies on highly mobile species have established that spatially static PAs are not the most effective conservation measure (Runge et al., 2014; Thirgood et al., 2004). For wide-ranging species, where PAs alone are not sufficient for their conservation, a number of dynamic conservation concepts have been suggested: (a) mobile PAs, (b) PA networks, (c) biodiversity offsets and (d) landscape-level management. Mobile PAs aim to temporarily protect areas where animals are known to aggregate (Taillon, Festa-bianchet, & Côté, 2012). These areas may shift along predictable changes of suitable habitats through the year. Likewise, PA networks aim to conserve critical areas along movement corridors or spatially predictable core refuges, like breeding and wintering areas (Roshier, Robertson, & Kingsford, 2002; Singh & Milner-Gulland, 2011). Both mobile PAs and PA networks depend upon locations that are known to be important at some point throughout the year. In contrast, biodiversity offsets are location-based approaches with the underlying idea that detrimental landscape modifications can be offset by conservation measures in different, spatially distinct areas of impact (Bull, Suttle, Singh, & Milner-Gulland, 2013; Gordon, Bull, Wilcox, & Maron, 2015).

With nomadic movements, however, an entire region is interconnected over the course of several years. Thus, while any of the aforementioned approaches can be important components of a

conservation strategy, for nomadic species, landscape-level management that considers all parts of the landscape is key to ensuring permeability across the entire landscape (Kremen & Merenlender, 2018; Poiani, Richter, Anderson, & Richter, 2000). Maintaining permeability throughout the entire landscape is critical for nomadic species to cope with the patchy and ephemeral distribution of resources and to avoid adversely affected areas during extreme conditions. For example, during our study period, a regional drought in the summer of 2015 was followed by an extremely cold and snowy severe winter (Rao et al., 2015): our movement data showed that some gazelle escaped the most severe winter conditions by moving long distances to the northeast, crossing the frozen Kherlen River (Figure S2, Animation S1). Evidence from other ungulate species during severe winter conditions shows that if large-scale escape movements are not possible, dramatic population declines can result (Kaczensky et al., 2011). Therefore, a key question for conservation is how permeability across the entire landscape can be maintained, especially in the face of infrastructure developments (Ascensão et al., 2018).

A critical issue for landscape permeability is linear infrastructure that can prevent nomadic species from accessing unpredictable and ephemeral resources across an entire landscape. For gazelle and other wide-ranging ungulates around the world, the negative effect of linear infrastructure such as fences, highways, and railroads is widely observed in barrier effects that cut off entire areas of the landscape where animals might have to move to escape harsh conditions or access migration routes and seasonal ranges (Ito, Lhagvasuren, et al., 2013; Wingard, Zahler, Victorine, Bayasgalan, & Bayarbaatar, 2014; Xia, Yang, Li, Wu, & Feng, 2007). In our case, the fence along the national border cannot be crossed by gazelle (Figure 1, Animation S1), and the movements of 80% of the 22 tracked individuals were affected by the border fence. When approaching the border fence, gazelle movements were extremely variable with regard to finding a crossing; some gazelle moved extended periods along the border fence, while others immediately gave up and moved away. In addition, several previous studies have shown that fencing causes high mortality in gazelle and other wide-ranging large mammals throughout Eurasia (Ito et al., 2008; Linnell et al., 2016; Olson, Mueller, Leimgruber, et al., 2009). Migratory ungulates that face habitat fragmentation and barrier effects often exhibit significant population declines or have perished altogether (Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009; Wilcove & Wikelski, 2008).

Identifying suitable design, spacing and locations for crossing structures and movement corridors along the migration routes are a mitigation measure for minimizing the landscape-scale impacts of linear barriers on migratory ungulates (Bastille-Rousseau, Wittemyer, Douglas-Hamilton, & Wall, 2018; Sawyer, Lebeau, & Hart, 2012). This conservation mitigation relies on areas repeatedly used by migratory ungulates, which show strong fidelity to routes and seasonal ranges. In contrast, nomadic species are difficult to manage because their key areas and seasonal ranges are not clearly defined and they do not exhibit repeated use of same locations. In wide-open

ecosystems in arid environments, such as the Eastern Steppe and the Kazakh Steppe, where gazelle and saiga antelope *Saiga tatarica* occur, respectively, identifying critical corridors and crossings is challenging because nomadic populations require such large expanses of habitat.

4.3 | Conservation of the Eastern Steppe

The Mongolian government proposed 5,683.5 km of new railways and road corridors across the core ranges of several ungulates, including gazelle (Figure 1, Animation S1; Batsaikhan et al., 2014; Gansukh et al., 2018). Any development projects are required to conduct environmental impact assessments in Mongolia (Law of Mongolia on Environmental Impact Assessments, 2011), and Mongolia has approved the wildlife crossing standard for road and railroads (Mongolian National Standard, 2015), which states that the locations of crossing structures must be selected based on scientific knowledge on animal movements and their movement corridors. While these mitigation standards and guidelines exist, there is a clear lack of strategy for implementation and recommendations based on scientific knowledge.

We show that gazelle avoid population centres, areas with a high density of roads, oil extraction fields and large-scale intensive agriculture (Figure 3, Animation S1). In addition, disturbances such as the proposed railway in the Eastern Steppe will fragment the steppe (Figure 1, Animation S1) and will become an impermeable barrier to gazelle movements if fenced. Avoiding or minimizing any landscape-scale impacts from infrastructure development on the permeability of the steppe should be a development planning priority.

An impediment to that goal is the lack of a region-wide comprehensive land-use plan. The Eastern Steppe is under the stewardship of multiple owners and is subject to a variety of management practices and regulations. Currently, different government agencies (e.g. Ministry of Food and Agriculture, Ministry of Mineral and Energy Resources, Ministry of Infrastructure and Development, Ministry of Environment and Tourism) as well as private sectors (e.g. extractive industries, transportation companies) that are dedicated to land development often act without considering landscape permeability and the conservation of wide-ranging animals.

We emphasize that the Eastern Steppe remains one of the largest and least fragmented temperate grasslands in the world and a stronghold of the largest remaining population of open plains ungulates world-wide and that their large-scale nomadic movements are recognized by the Convention of Migratory Species. The ecological integrity of the steppe can be preserved, where gazelle continue to benefit from unrestricted access throughout the landscape by limiting infrastructure expansion. This could be achieved by designating the regions of the steppe currently categorized as "pasture" and "management" via traditional land use practices as an IUCN category V protected landscape, where conservation objectives are set across large areas and the management is carried out by a range of actors (Dudley, 2008). Such a designation could help preserve

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Nandintsetseg D, Bracis C, Olson KA, et al. Challenges in the conservation of wide-ranging nomadic species. *J Appl Ecol*. 2019;00:1–11. <https://doi.org/10.1111/1365-2664.13380>

Supporting Information for manuscript of Challenges in the conservation of wide-ranging nomadic species**Table S1.** Metadata for GPS movement data and annual ranges of Mongolian gazelle.

In October 2014, 12 gazelle were fitted with GPS collars at a single location (sample 1) and in September 2015, 10 gazelle were fitted with GPS collars in the course of two weeks at four locations (sample 2) (see the capture locations in Figure S2). Adult gazelle were fitted with two different types of GPS collars. Due to our multiple-years monitoring effort into nomadic movements, we used Lifecycle GPS collars from Lotek for 17 gazelle, which were programmed to transmit one location every 23 hours. In addition, for five individuals, we tested solar assist GPS Iridium collars from Sirtrack, which were programmed to transmit one location every hour. To standardize the analysis, we sub-sampled the hourly location data into mix of 23 and 24 hour intervals using the “SyncMove” R package. Further details on fix schedules, the number of days each individual was monitored, and the number of recorded locations for each individual, are provided in the table below. The analyzed data set consisted of 12,166 daily GPS points of 22 individuals (19 females and 3 males).

#	Animal ID	Sex	Sample	Monitoring period		Number of fixes/days				Annual range size, km (95% MCP)		
				Start	End	Total	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
1	36654	F	1	16/10/2014	16/10/2015	289	289	-	-	6,431	-	-
2	36655	F	1	16/10/2014	4/9/2016	375	223	152	-	19,405	10,252	-
3	36656	F	1	16/10/2014	14/10/2016	479	271	208	-	13,201	19,790	-
4	36657	F	1	16/10/2014	12/10/2017	876	310	298	268	20,213	23,114	26,986
5	36659	F	1	17/10/2014	12/10/2017	840	331	276	233	9,493	24,927	14,445
6	36660	F	1	16/10/2014	1/10/2017	853	330	313	210	13,189	9,209	11,564
7	36661	F	1	16/10/2014	15/10/2016	592	307	285	-	13,246	16,691	-
8	36662	F	1	16/10/2014	16/10/2015	272	272	-	-	15,097	-	-
9	36663	F	1	15/10/2014	13/10/2017	834	307	276	251	19,564	31,044	17,127
10	36666	F	1	16/10/2014	16/10/2015	296	296	-	-	16,743	-	-
11	36667	F	1	16/10/2014	14/10/2015	312	312	-	-	7,771	-	-
12	61561370	F	1	17/10/2014	16/10/2017	1035	328	356	351	24,849	53,422	17,890
13	39234	F	2	9/9/2015	6/9/2017	664	337	-	327	24,177	21,043	-
14	39238	F	2	7/9/2015	6/9/2017	690	356	-	334	11,899	6,853	-
15	39246	M	2	10/9/2015	9/9/2016	373	373	-	-	22,985	-	-
16	39249	M	2	9/9/2015	8/9/2017	719	368	-	351	37,447	12,696	-
17	39250	M	2	12/9/2015	11/9/2016	362	362	-	-	10,616	-	-
18	366642	F	2	12/9/2015	10/9/2016	200	200	-	-	17,283	-	-
19	62676240	F	2	11/9/2015	10/9/2017	727	363	-	364	19,018	29,838	-
20	62679240	F	2	12/9/2015	11/9/2016	367	367	-	-	27,149	-	-
21	62940480	F	2	12/9/2015	11/9/2016	322	322	-	-	25,680	-	-

22	62947480	F	2	9/9/2015	8/9/2017	689	324	-	365	187,450	32,759	-
						1216						
Total location						6						

Description S1. Simulation model methods.

We generated correlated random walks (CRW) by drawing the step length and turning angle from the empirical distributions of GPS tracked gazelle. We simulated movement paths using each individual's time step and duration, and then removed locations from the full simulated trajectories corresponding to the gaps in the empirical movement paths (Table S1) resulting in the same number of data points between simulated and empirical paths. We bounded simulations by the border of Mongolia and the existing Trans-Mongolian Railway fences (Figure S2) which restrict gazelle movements. We simulated 1000 replicates for each individual. We used the simulated movement paths as a null movement model, in which direction is persistent, but there are no habitat preferences and no tendency to return to previously visited areas. We used a randomization test (Ernst, 2004) to assess the statistical significance of the three objectives with the empirical data as described in more detail below. We estimated p-value (s) for a one-sided test:

$$\hat{p} = \frac{1 + \sum_{i=1}^n I(x_i \geq x^*)}{n + 1}$$

where n is the total number of randomization simulations and I is the indicator function, and we counted the number of times the sampled x_i is more extreme than our observed value, x^* . To note that in some cases, the one-sided was the other direction, $x_i \leq x^*$, to count random samples smaller than our observed value. For example, we assessed whether tagged gazelle used protected areas more often than simulated ones and whether the disturbance index for areas gazelle traveled through was lower than that of simulated ones.

Animation S1. The animation of gazelle movements is provided as MPEG file for the submission of the manuscript. The animation is submitted as supplementary material and is attached as the link below.

<https://www.dropbox.com/sh/yskeojnpd5ykuis/AABwZQOIve2QzP8cviYOip4a?dl=0>

Table S2. Movement parameters and lifetime range sizes of GPS-tagged Mongolian gazelles in the Mongolian steppe.

Lifetime ranges were estimated via Autocorrelated Kernel Density Estimates (AKDE)

Animal ID	Number of fixes	of Range crossing time (months)	Average distance traveled (km/day)	Lifetime AKDE (km ²) (95% CI)	range
36656	479	1.9	9.5	39,438 (21,625 - 62,514)	
36657	876	7.0	10.8	123,260 (48,432 - 232,429)	
36659	840	3.9	9.1	58,228 (28,848 - 97,752)	

36660	853	6.1	8.7	77,377 (31,908 - 142,636)
36661	592	3.9	8.6	58,844 (25,265 - 106,373)
36663	834	6.5	9.9	114,520 (45,049 - 215,838)
39234	664	7.7	9.9	117,700 (30,708 - 262,052)
39238	690	3.5	8.6	38,100 (16,790 - 67,990)
39249	719	9.3	11.0	158,178 (32,252 - 382,278)
61561370	1035	6.8	11.7	144,677 (58,741 - 268,671)
62676240	727	6.5	13.0	167,840 (53,676 - 345,916)
62947480	689	4.9	11.6	112,182 (43,953 - 211,818)

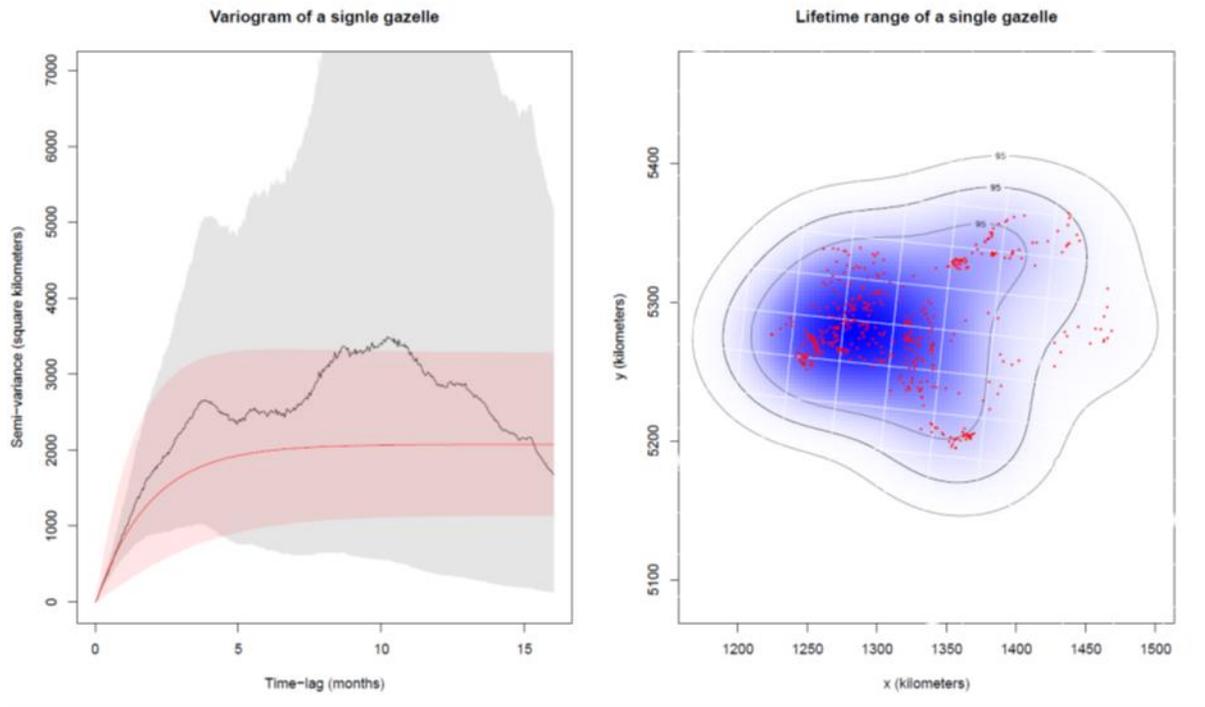


Figure S1. Example variogram and lifetime range of a single gazelle.

(A) Notice that the gazelle's semi-variance reaches an asymptote within two months, roughly representing the time to cross its range for the particular individual shown here. The red line represents the fitted model and the red shading represents the 95% CI. The time fraction of the variogram displayed is 65% of the duration of the tracking data. **(B)** The lifetime range estimate (AKDE), which conditions on the selected model using the variogram. The red points are the actual movement data. The middle contour represents the maximum likelihood area where the gazelle spent 95% of its time (i.e. the values reported in this manuscript). The inner and outer contours correspond to confidence intervals on the magnitude of the area.

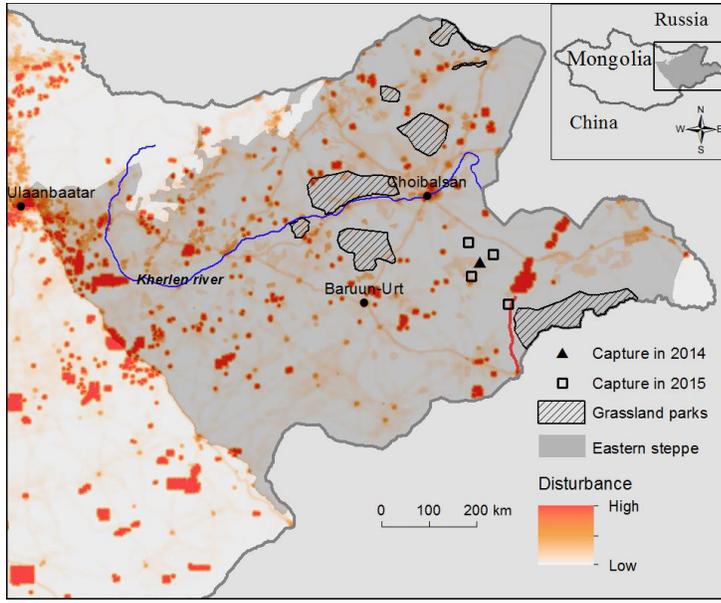


Figure S2. The core range of Mongolian gazelle, which is restricted by fences along the Trans - Mongolian Railroad and the national border.

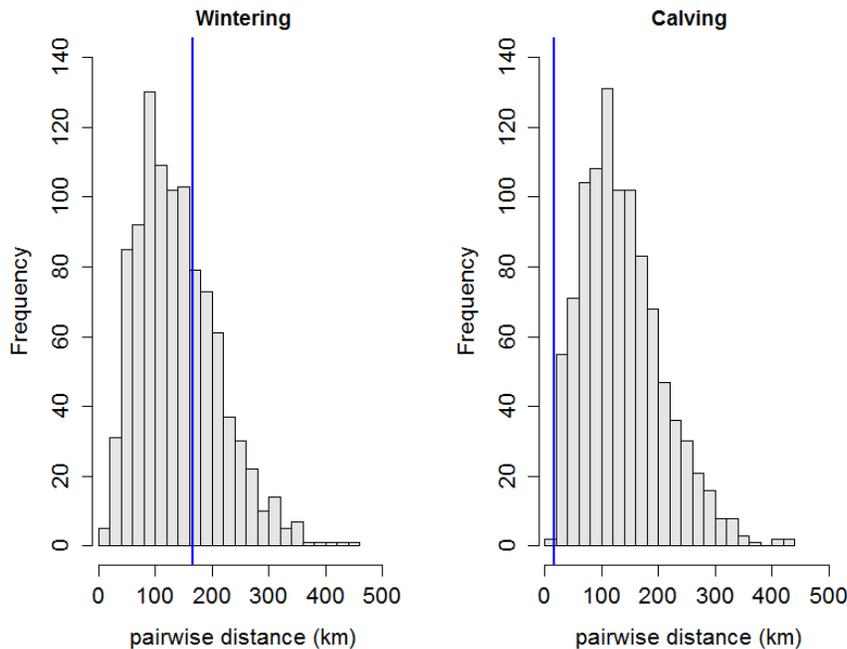


Figure S3. An example comparison of mean pairwise distances of a single tagged gazelle with those of the simulation null model for wintering and calving periods. The histogram represents the distribution of mean pairwise distance from the 1000 simulations and the blue line represents the mean pairwise distance of a single tagged gazelle. The null distributions of the pairwise distances during both the wintering and calving periods are compared to the mean pairwise distances of a single tagged gazelle. For wintering periods, the mean pairwise distance of the individual gazelle was not significantly different than the null

distributions ($\hat{p} = 0.67$), but for calving periods, there was a significance difference ($\hat{p} = 0.002$), which indicates that this individual gazelle did show site fidelity during calving time. However, this pattern was not consistent across all individuals: mean pairwise distances of most of tagged gazelles were not significantly different than the null distributions for calving periods (see Table S3).

Table S3. Individual difference in the predictability of space use during wintering and calving periods

We examined the predictability of space use for each individual based on pairwise distances between years. We compared the wintering and calving mean pairwise distances of the tagged female gazelles to the simulation null model. We then estimated the p-value for each individual for both wintering and calving periods. Note that for winter, all individuals' pairwise distances were not significantly different than the null model, which indicate gazelles do not have wintering site fidelity. Contrary to this pattern, there was individual level variability in the predictability of space use during calving periods and the mean pairwise distances of three individuals were significantly different than the null model (in bold).

Animal ID	Wintering	Calving
	\hat{p} -value	
36655	0.248	0.394
36656	0.696	0.002
36657	0.972	0.519
36659	0.753	0.256
36660	0.929	0.313
36661	0.432	0.159
36663	0.441	0.022
61561370	0.093	0.276
39234	0.438	0.286
39238	0.962	0.018
62676240	0.972	0.752
62947480	0.876	0.440

A.3 Variability in nomadism: Environmental gradients modulate movement behaviors of dryland ungulates

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(1) Concept and design

Doctoral candidate ND 90%
Co-author TM 10%

(2) Conducting tests and experiments

Doctoral candidate ND 25% (GPS movement data for Mongolian gazelle)
Co-authors PK, JP, CW, BB, BC, SE, TI, MS and BL 75% (GPS movement data for four ungulate species)

(3) Compilation of data sets and figures

Doctoral candidate ND 100% (compiling raw GPS movement data across four species and preparing all figures).

(4) Analysis and interpretation of data

Doctoral candidate ND 85% (all analyses including calculating various movement metrics, ordination analyses, obtaining remote sensing data, and regression analyses, as well as the interpretation of data).

Co-authors TM and CB together in total (10%) advised on the data analyses and interpretation on data. Co-author NH (5%) advised on obtaining environmental data across the study system in Mongolia.

(5) Drafting of manuscript

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All co-authors helped revising the manuscript 5%

Article title: Variability in Nomadism: Environmental Gradients Modulate the Movement Behaviors of Dryland Ungulates.

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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- versus 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 (PCA) to quantify the variation in movement patterns. The satellite-derived vegetation greenness (NDVI) served as a proxy for the resource gradient and was associated with the variation in movement behaviors described in the first principal component demonstrating that the variability in movements was closely related to the resource gradient along the mesic and xeric conditions. 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 ecosystems 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, ungulate, arid, nomadism, forage, water, resource, recursion

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 weather events (Greenville et al., 2012; Jordan et al., 2017; Kaczensky et al., 2011a; Szymkowiak and Kuczyński, 2015). 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 broad-scale patchy resources (Fryxell et al., 2004; Roshier et al., 2008a). In arid environments, key resources are water and forage, which are often temporally variable, but can be relatively static or dynamic in their locations. In desert and semi-deserts, water is often a key resource and animals have to drink regularly or rely on food abundance derived from water availability. Water availability at ephemeral oases and wetlands is temporally unpredictable, but their spatial location is often relatively static. The unpredictable changes in the water availability could lead to “water-driven nomadism”. For example, the gray teal *Anas gracilis* in Australia, a nomadic waterbird, has been shown to move long distances to track high food abundance in response to infrequent wetland flooding events (Roshier et al., 2008a). In contrast, ephemeral, broad-scale foraging patches can drive “forage-driven nomadism”, where animals track broad-scale patches with suitable food resources. Their spatial location may less depend on topographic features but much more depend on ephemeral rainfall events, and in consequence 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 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 ranges from Mongolia’s vast relatively mesic grassland steppe in the east to deserts and semi-deserts (hereafter deserts) further west and is characterized by low and variable rainfall in space and time (Khishigbayar et al., 2015; Vandandorj et al., 2015). It 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* (Batsaikhan et al., 2014; Buuveibaatar et al., 2016b; Young et al., 2010) (Figure 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 steppe to desert in the Gobi-Steppe Ecosystem. We used movement metrics, including displacement distances and recursion metrics, which have previously been useful in classifying broad-scale 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.

Study species and region

The Gobi-Steppe Ecosystem in Mongolia covers an area of 827,000 km² across eastern, southern and south-western Mongolia (Batsaikhan et al., 2014) and encompasses the distribution range of our four study species (Figure 1). In this arid and semi-arid ecosystems, 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 south-west are characterized by semi-desert and desert ecosystems. The elevation in the eastern steppe ranges from 800 m to 1300m, increasing toward 1800 m in the southern Gobi desert (Buuveibaatar et al., 2013; Imai et al., 2017; Kaczensky et al., 2011b).

The steppe is characterized by cold steppe climate with a lack of surface water and average annual precipitation of 300 mm (Greenville et al., 2012). 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, vegetation growing season. The eastern steppe provides critical habitat for the largest population of Mongolian gazelle in the world (Mallon, 2008).

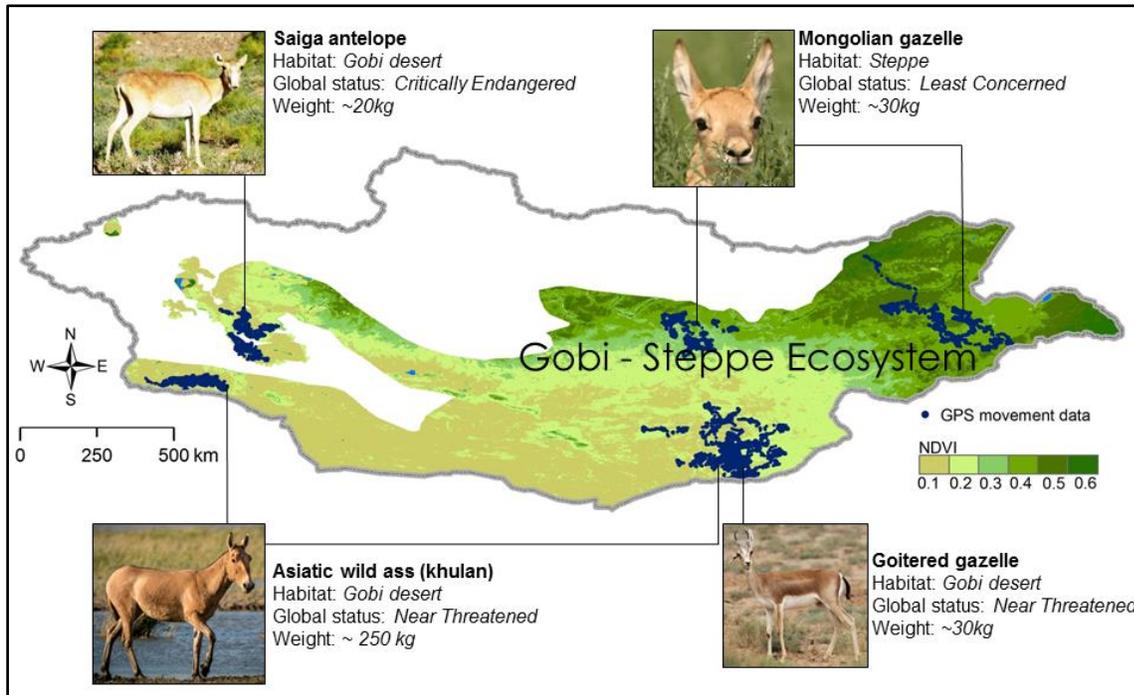


Figure 1. The joint distribution range of wide - ranging ungulates occupying the Gobi-Steppe Ecosystem in Mongolia. The distribution range for each species is derived from IUCN assessments. GPS movement dataset from the four study species is highlighted in blue. The background image shows the distribution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

The Gobi desert is characterized by a cold desert climate and average annual precipitation ranges from 50 mm up to 200 mm (Kaczensky et al., 2011b). The Gobi desert is an open shrubland where vegetation is sparse with barren ground, and 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 polyrrhizum*). 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 in the Mongolian Gobi desert, it supports the largest remaining population of khulan and goitered gazelle in the world (Buuveibaatar et al., 2016b). In addition,

the Gobi desert supports a small population of a distinct subspecies of the critically endangered saiga antelope (Greenville et al., 2012).

Methods

GPS movement data

We compiled GPS movement data of 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 minutes to every 4 hours or every 5 hours. To standardize movement data across individuals, we resampled all data to a 4-hour interval except for three individual saiga antelopes that were sampled at a 5-hour interval (Table S1 in Appendix). Given our research interest in forage versus 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 had to use 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, 6 goitered gazelle, 15 khulan, and 8 saiga antelopes, with individual numbers of GPS locations ranging between 539 and 732 (Table S1 in Appendix).

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 time scales and three recursive movement metrics.

Displacement distances

We calculated 1-day and 10-day displacement distances for each individual using the “Move” R package (Bart et al., 2018). The 1-day displacement (hereafter daily displacement) was calculated as the distance between two consecutive GPS positions 24 hours apart except for the three individuals saiga antelopes where locations were 25 hours apart. We were also interested in the displacement over longer time frames. Following Tucker et al (2018), we additionally calculated the 10-day displacement as the distance between two consecutive GPS positions 10 days 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., 2017b). 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 (Bracis et al., 2018), 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.

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, see details below) centered on the focal GPS location. Step length was calculated as the Euclidean distance between consecutive GPS locations with 4-hour intervals and the median step length was 0.79 ± 1.55 km (median \pm SD) for Mongolian gazelle, 0.73 ± 1.22 km for goitered gazelle, 0.96 ± 1.81 km for saiga antelope, and 1.20 ± 2.31 km for khulan respectively (Figure S1). The median step length across all species was nearly 1 km, leading us to select a radius of 1 km. We then set a threshold time of 8 hours (see details below) to eliminate brief excursions from the defined-circle, 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 hours 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 (Figure S2) and threshold times of 4-, 8-, and 12-hour (Figure S3). Eventually the number of revisits starts to decrease at the 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-hours (Figure S3 and S4).

We calculated mean daily and 10-day 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 tests (ANOVA) 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 (Table S2). Next we used the Tukey Honest Significant Differences (Tukey HSD) test to determine which pairs of species were significantly different from each other in the case that the ANOVA result was significant with the *TukeyHSD* function in the ‘Stats’ R package.

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 to explore any underlying patterns in the movement metrics across species. All movement metrics were first log-transformed. To choose which PCA axis best explains 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, Figure 3).

Foraging resource availability

We used NDVI (Normalized Difference Vegetation Index) as a proxy for vegetation availability to examine whether the gradient from the more mesic steppe to the xeric desert explains any of the variability in movement behavior detected in the PCA. The NDVI data were obtained from the 16-Day 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 was collected, resulting in 95 composite images. For each pixel, we calculated the mean of NDVI across the 95 composites, indicating the 12-year average vegetation availability between April and July across the Gobi-Steppe Ecosystem. We annotated GPS locations with the NDVI values and then averaged values for each individual. We used linear-mixed effects models to predict the relationship between the NDVI gradient and the variability in movement behavior as a dependent variable based on the first PC axis. Species were included in the model as a random factor. 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.

Results

Variability of movement behavior across ungulate species

We found significant differences in the movement metrics across species (Figure 2a-e and Table S2).

For *daily displacement*, goitered gazelle in the desert had the shortest daily displacement (2.3 ± 0.8 km; mean \pm SD), significantly shorter than any of the other three species (Figure 2a, 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 (Figure 2a).

For *10-day displacement*, the longer time scale, showed 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) (Figure 2b, 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-day displacement of khulan was over 4 times longer than goitered gazelle and 2 times longer than saiga antelope, and that of Mongolian gazelle was 3 times greater than goitered gazelle (Figure 2b, Table S2).

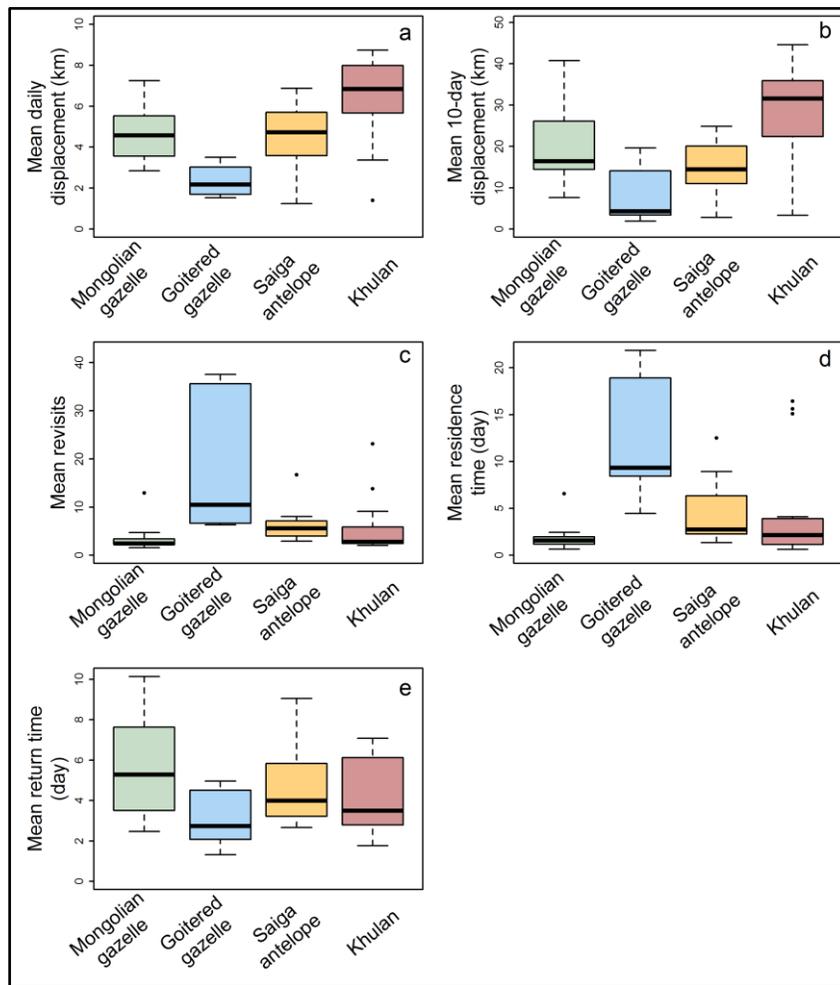


Figure 2. Movement metrics of four ungulate species in the Gobi-Steppe Ecosystem in Mongolia. The movement metrics showed that khulan living in the desert and Mongolian gazelle living in the steppe were the most similar to each other (Table S2). They had longer displacement distances and fewer revisits. 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.

For *revisit rate*, goitered gazelle had a mean revisit rate of 17.8 ± 14.6 times (mean \pm 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 (Figure 2c, Table S2). For *residence time*, there was a similar pattern as the revisitation rate (Figure 2d, Table S2). Due to the frequent revisits, goitered gazelle had a long mean residence time of 12.0 ± 6.8 days (mean \pm SD) in a specific area. In contrast, Mongolian gazelle had a mean residence time of 1.9 ± 1.6 days, 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 days (mean \pm SD) for goitered gazelle, 4.7 ± 2.8 days for saiga antelope, 4.2 ± 1.9 days for khulan, and 5.8 ± 2.8 days for Mongolian gazelle (Figure 2e, Table S2).

Table 1. Contributions of movement metrics to each principal components and cumulative percentage of variance explained by PCA.

Movement metrics	PCA components				
	PC1	PC2	PC3	PC4	PC5
Daily displacement	-0.48	-0.09	0.61	-0.29	-0.54
10-day 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%

The first two principal components (PC) of these movement metrics explained 91.0% of the variance among the movement metrics for the four ungulate species (Table 1, Figure 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-day displacement distance (Table 1, Figure 3). The second PC (PC2) explained 18.1% of the variance and was positively correlated with return time (Table 1, Figure 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.

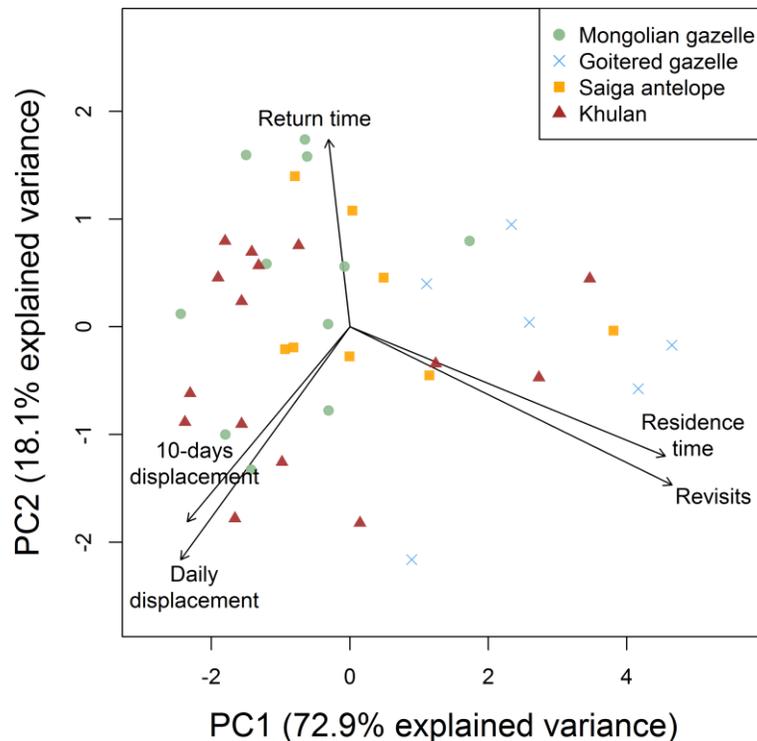


Figure 3. Relationship of movement metric PC1 and PC2 for each individual.

Variability in movement behavior in relation to the availability of vegetation

The linear mixed-effects model showed vegetation availability (NDVI) was a significant predictor of the variability of nomadic movement behavior (PC1), explaining approximately 21 % of the variance in PC1 of the movement metrics (Figure 4, 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, in less vegetated xeric desert habitats, individuals moved shorter distances with more frequent revisits to previously visited areas (Figure 4).

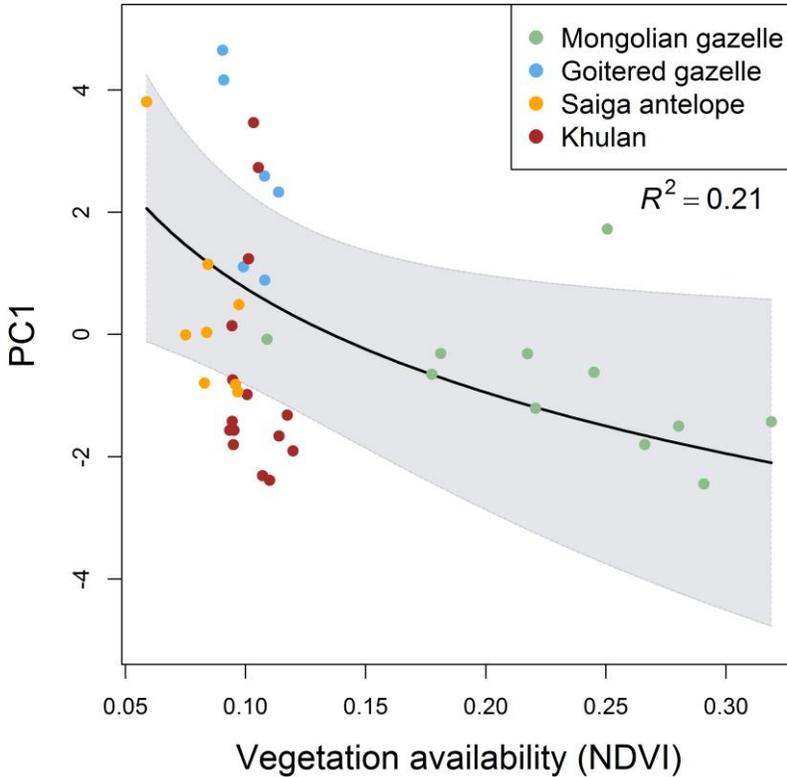


Figure 4. The relationship between nomadic movement behavior and a gradient of vegetation availability in the Gobi-Steppe Ecosystem. The grey area represents the 95% confidence interval for the predicted values. PC1 characterizes the movement behavior from long distance movements with few revisits to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

Discussion

Our results showed that the wide-ranging ungulate movements of four species across the Gobi-Steppe Ecosystem varied between long distance movements with infrequent revisits and short distance movements with frequent revisits to previously visited areas (Figure 3). This variability in movement behaviors is partially explained by the gradient of vegetation availability (Figure 4) and in the mesic steppe with greater vegetation availability nomadic movement behavior is characterized by longer movements with infrequent revisits to previously used areas (Figure 4). In contrast, in the desert, the movement behavior was characterized by shorter distances and more frequent revisits. Overall, this pattern supports our initial hypotheses differentiating forage-driven nomadism tracking broad scale and spatially unpredictable foraging resource in mesic steppe compared to 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 that shows in resource-poor arid environments, animals move longer distances than the 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 on arid environments from grassland steppes to 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 (Figure 2). Mongolian gazelle in the steppe (herbaceous grassland) with more vegetation, for instance, moved nearly three times further than similar-sized goitered gazelle in the desert (open shrubland) at a 10-day 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 that allow 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 (Fagan et al., 2013; Mueller and Fagan, 2008). 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 similar findings that animals move faster in more heterogeneous landscapes to increase encounters with the locations of foraging areas (Avgar et al., 2013). 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 good foraging areas in the mesic grassland steppe.

In the resource-poor deserts landscapes of the Gobi steppe ecosystem, 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 arid and semi-arid ecosystems 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 central places where animals must return to periodically resulting in constrained movements of water-dependent species (Bleich et al., 2010; Rozen-Rechels et al., 2015). For example, feral horses in Sable Island National Park in Canada occurred close to water sources during summer time (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 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 conditions modulates return movements, we emphasize that due to our broad scale study region with sparsely distributed ephemeral water sources, we were not able to validate that recursive movements were indeed to waterbodies.

In addition, movement metrics showed significant among species variability even within the xeric desert environment (Figure 2). In particular, goitered gazelle had the highest mean revisits and residence time and the shortest displacement distance for both daily and 10-day displacements, suggesting goitered gazelle return often to only a few specific areas. By comparison, saiga antelope, a similar sized ungulate in the desert, is more mobile and showed less 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., 2010b), water usage and its effects on their movements has been little studied. 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, are dependent on more or less daily access to water sources and distance to water is an essential factor in habitat use (Buuveibaatar et al., 2016a; Kaczensky et al., 2010; Nandintsetseg et al., 2016). However, khulan are capable of accessing water by digging in dry riverbeds in areas where the ground water table is high (Feh et al., 2001), which makes them independent from localized water sources. This may explain the high mobility of khulan in the desert environment, whereas goitered gazelle likely rely on permanent water sources because they are unable to access the ground water via excavating. Future research could examine whether goitered gazelle can follow movements of khulan for accessing ephemeral water sources in areas where both species co-exist.

We emphasize that the coarse sampling rate (4-h interval GPS fixes) and the four months' GPS movement dataset could have reduced the detection of recursive movement metrics. Animals might require more water or patches with high-quality water-rich green vegetation in August through October when vegetation becomes drier, but data was 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 that a longer-term and higher resolution dataset on movements of nomadic ungulate species would be helpful to better to 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 over years. It would also enable understanding whether nomadic ungulates reuse refugee areas during extreme climatic events, such as is observed in nomadic birds (Runge et al., 2016). With the 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 add more individuals and species to the data set. Especially for the mesic steppe environment we had only few individuals of Mongolian gazelles available and more individuals and species under mesic conditions would help to corroborate the pattern found here. Such studies should consider effects of resource heterogeneity, resource predictability, resource recovery rate, and animal's cognitive capabilities on recursion movements (Berger-Tal and Bar-David, 2015). Finally, there are a number of additional factors that potentially may influence recursion movement metrics and that we did not investigate here. These include predator

avoidance, resting sites, social structure, and human-induced disturbance (Benhamou and Riotte-Lambert, 2012; English et al., 2014; Montpellier and Centre, 2008).

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 semi-arid ecosystems, nomadic movement behavior may differ across resource gradients. In the resource-rich mesic steppe with temporally unpredictable foraging resource, 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 are 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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Author contributions: ND conceived and designed the study, performed all analyses, and led writing contributions from TM and CB. PK, BB, CHB and TI contributed the GPS movement dataset for khulan, saiga antelope and some individuals of Mongolian gazelle. NH contributed to obtaining the remote sensing imagery across the study system. All authors participated in the discussion of writing and reviewing of the manuscript, and provided final approval for publication.

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Supplementary material for A.3

Table S1. GPS movement dataset for calculation of movement metrics

Species	Individual ID	Habitat	Sex	Monthly GPS positions				Total
				April	May	June	July	
Mongolian gazelle (<i>Procapra gutturosa</i>)	61561370	Steppe	F	180	186	180	186	732
	62676240		F	180	186	180	186	732
	62940480		F	180	186	180	185	731
	62947480		F	180	186	180	186	732
	62674330		F	180	186	180	186	732
	62943640		F	180	186	180	186	732
	62946690		F	180	186	180	186	732
	63995810		F	179	185	180	186	730
	64520520		F	180	186	180	186	732
	64525510		F	180	186	180	186	732
	64527510		F	180	186	156	186	708
Goitered gazelle (<i>Gazella subgutturosa</i>)	60593620	Gobi desert	F	180	186	180	186	732
	61152400		F	171	183	180	186	720
	61157410		F	140	166	169	184	659
	61320910		M	180	186	180	186	732
	61561400		M	178	185	180	186	729
	61564490		F	180	185	180	186	731
Khulan (<i>Equus hemionus</i>)	13549	Gobi desert	F	180	186	180	186	732
	13557		F	180	186	180	185	731
	13741		M	179	186	180	186	731
	13743		M	180	185	179	184	728
	13744		F	180	186	179	186	731
	13745		F	180	186	180	186	732
	13747		M	180	186	179	186	731
	34407		M	180	185	179	185	729
	34413		M	180	186	179	185	730
	3		F	180	186	180	116	662
	4		M	176	182	174	113	645
	7		M	166	173	168	107	614
	6441		M	180	186	180	115	661
	6446		F	180	186	180	115	661
	7376		F	180	186	180	115	661
Saiga antelope (<i>Saiga tatarica mongolica</i>)	111	Gobi desert	F	135	146	137	146	564
	112		F	141	142	132	134	549
	113		F	133	139	131	136	539
	62060790		F	180	186	180	37	583
	62068770		F	180	186	180	36	582
	62670350		F	180	185	180	36	581
	62673340		M	180	186	179	36	581
	62679330		F	180	186	180	36	582
Total GPS positions							27368	

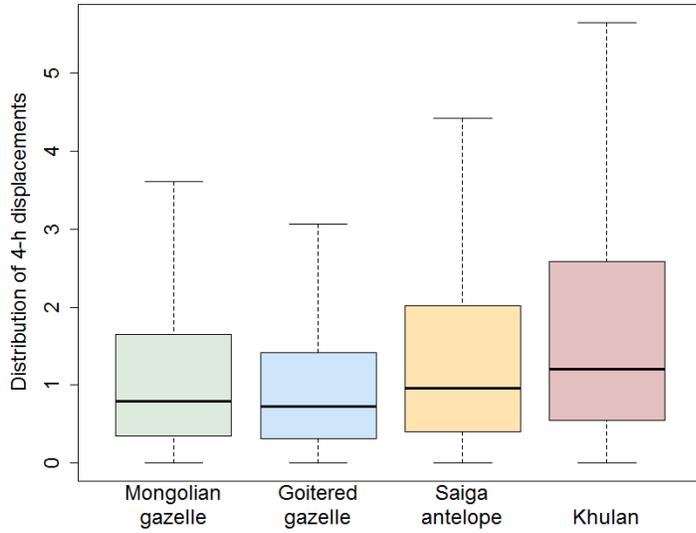


Figure S1. The distribution of 4-h step lengths across species. The median distance across species was ~ 1km that leads us to select radius of 1 km for recursion analysis.

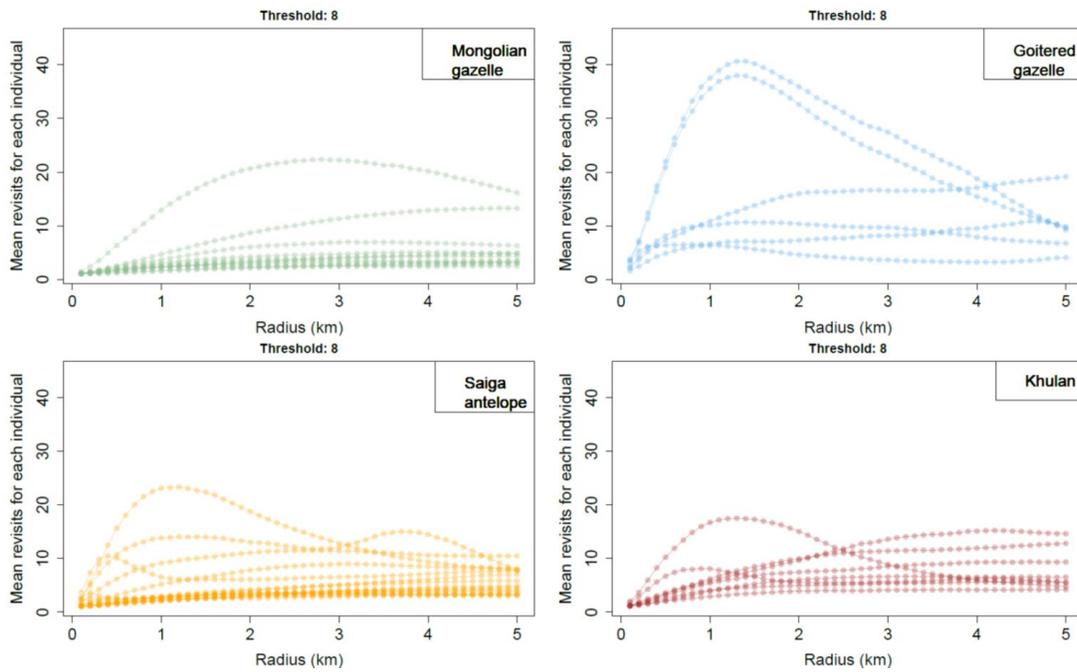


Figure S2. Recursion estimates at radii of 0.1 to 5 km in increments of 0.1 km.

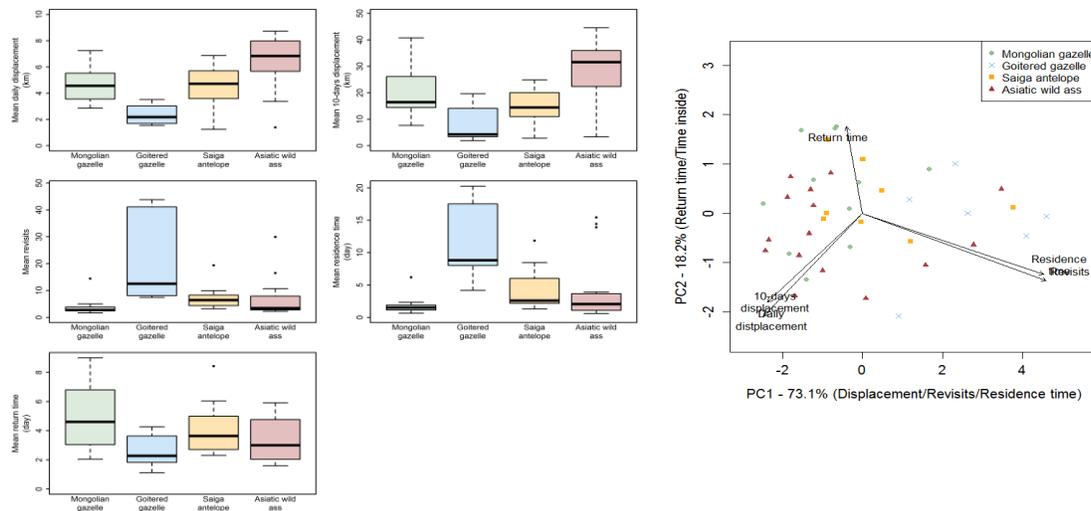


Figure S3. Movement metrics derived from radius of 1 km and 4-h threshold and the resulting relationship of PC1 and PC2 from the PCA.

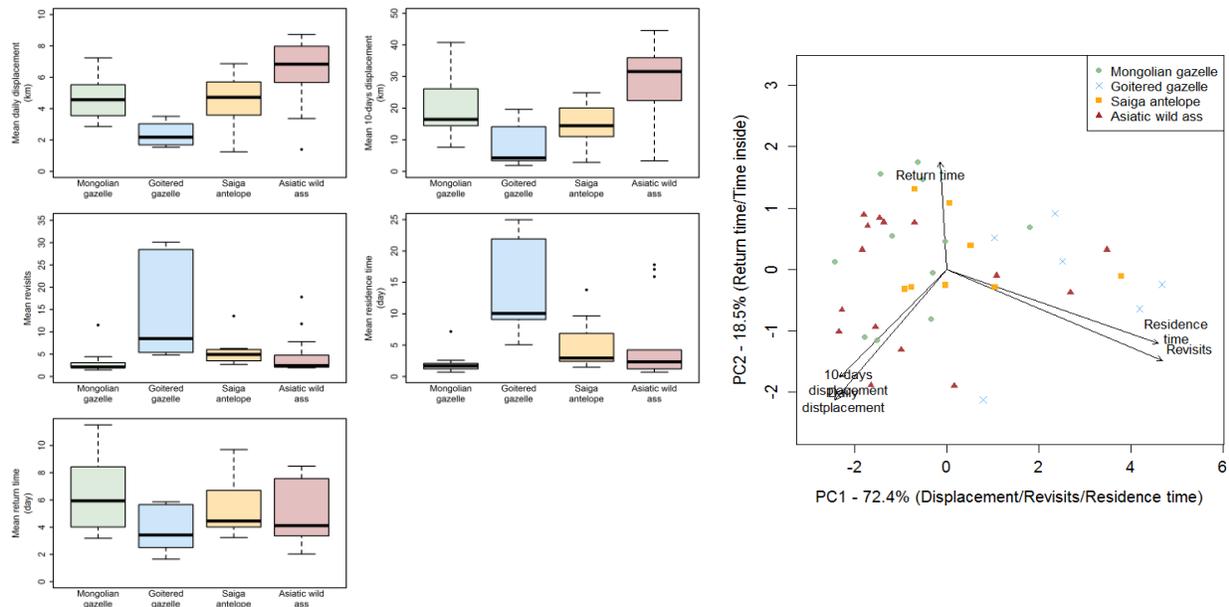


Figure S4. Movement metrics derived from radius of 1 km and 12-h threshold and the resulting relationship of PC1 and PC2 from the PCA.

Table S2. The one-way ANOVA test was significant for movement metrics of daily displacement ($F_{(3,33)} = 20.45, p < 0.05$), 10-day displacement ($F_{(3,34)} = 12.52, p < 0.05$), revisit rates ($F_{(3,36)} = 7.12, p < 0.05$), and residence time ($F_{(3,36)} = 5.76, p < 0.05$) indicating that some of group means are different. The ANOVA test was not significant for return time ($F_{(3,36)} = 2.32, p = 0.09$), indicating there were no statistically significant differences between species means for the return time. The pairwise comparisons between species for each of the movement metrics were performed using the Tukey post-hoc test. Significant codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. p-values are shown for non-significant comparisons. Note that we did not use Tukey post hoc analysis for return time because ANOVA test did not show significant difference among species.

Species	Daily displacement (km)		Species		
	Mean	Std. Deviation	Goitered gazelle	Saiga antelope	Khulan
Mongolian gazelle	4.6	1.4	***	0.93	***
Goitered gazelle	2.3	0.8		***	***
Saiga antelope	4.9	1.2			***
Khulan	7	1.3			

Species	10-day displacement (km)		Species		
	Mean	Std. Deviation	Goitered gazelle	Saiga antelope	Khulan
Mongolian gazelle	20.9	10.4	**	0.46	0.22
Goitered gazelle	7.9	7.1		0.05	***
Saiga antelope	14.8	6.9			*
Khulan	31	8.7			

Species	Revisits		Species		
	Mean	Std. Deviation	Goitered gazelle	Saiga antelope	Khulan
Mongolian gazelle	3.6	3.2	***	0.79	0.903
Goitered gazelle	17.8	14.6		*	**
Saiga antelope	6.6	5.9			0.98
Khulan	5.5	5.9			

Species	Residence time (days)		Species		
	Mean	Std. Deviation	Goitered gazelle	Saiga antelope	Khulan
Mongolian gazelle	1.9	1.6	***	0.65	0.502
Goitered gazelle	12	6.8		*	*
Saiga antelope	4.6	3.9			0.99
Khulan	4.6	5.8			

Species	Time to return (days)				
	Mean	Std. Deviation			
Mongolian gazelle	5.8	2.8			
Goitered gazelle	3	1.4			
Saiga antelope	4.7	4.2			
Khulan	4.2	1.9			

Table S3. Model coefficients, r^2 and sample sizes of linear mixed effects models predicting the variability in movement behavior. The predictor variable was NDVI and the random variable was species. We calculated the marginal r^2 (variance explained by the fixed effects) and conditional r^2 (variance explained by both fixed and random factors) values for the model using the “MuMIn” R package. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Covariate	Estimate	Std.Error	df	t value	p value
(Intercept)	-4.91	2.45	15.77	-2.002	0.06
log NDVI	-2.46	1.09	20.66	-2.25	0.03*
r^2 Marginal	0.21				
r^2 Conditional	0.59				
Species	4				
Individuals	40				