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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 km^2 and a lifetime range of ~100,000 km^2.
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.

KEYWORDS
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 km^2 in 1 year (Olson et al., 2010). The species' core distribution range in eastern Mongolia is 200,000 km^2 ± 3,100 km^2 (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, &

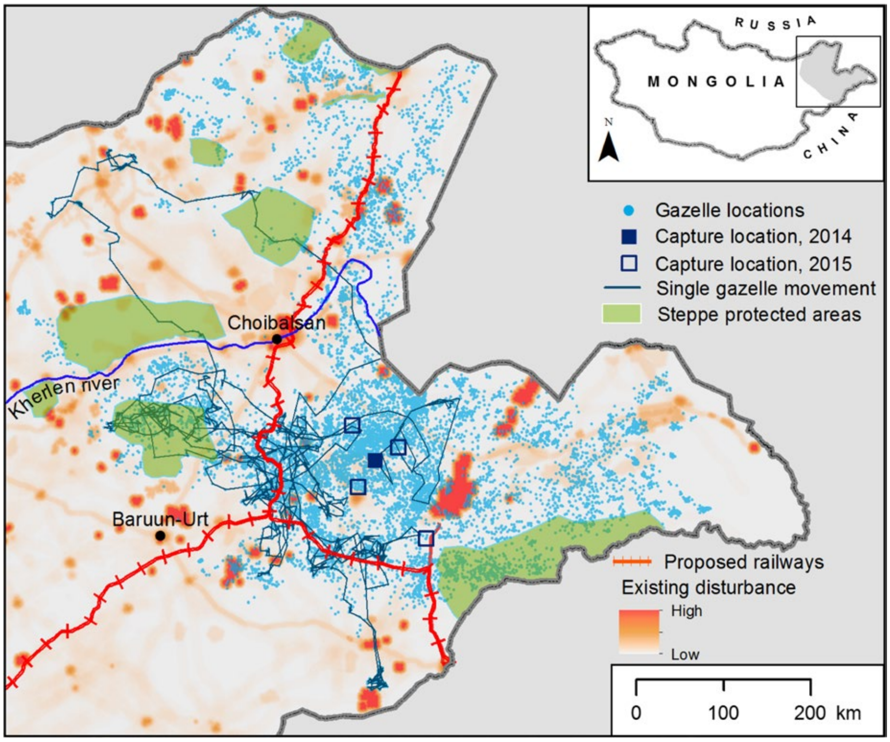

FIGURE 1 Mongolian gazelle GPS locations with existing and proposed disturbances and protected areas in the core range of Mongolian gazelle in Mongolia

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 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 km^2 (n = 40 annual ranges, Figure 2), but this varied greatly among individuals

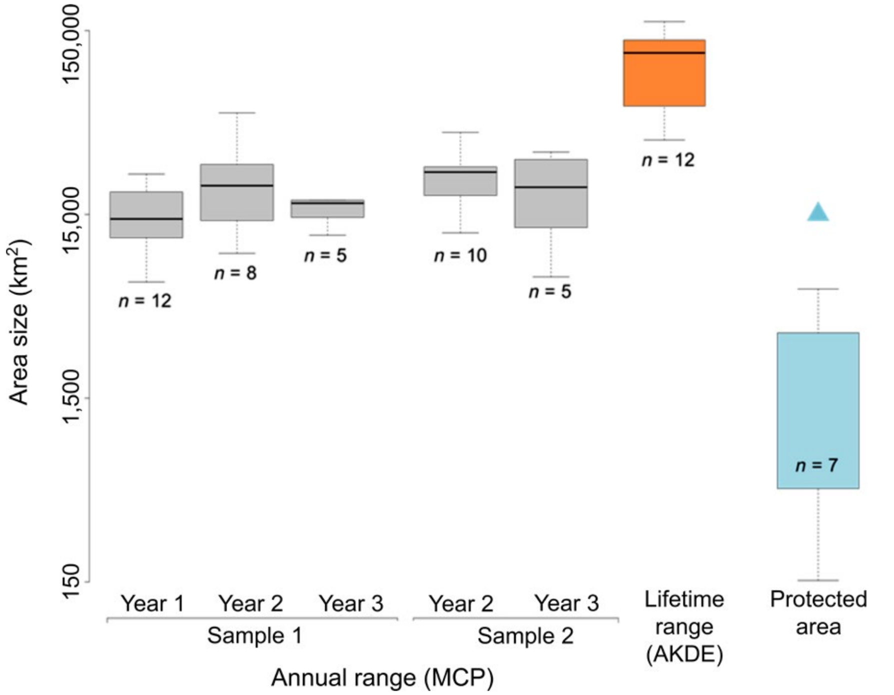

FIGURE 2 Annual range (MCP) and lifetime range estimations (AKDE) of individual Mongolian gazelle compared to the sizes of protected areas in the eastern Mongolia on a log scale. Not all individuals survived the entire study period and the sample size decreases with study years for both samples. The 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 km^2). The largest annual range (53,422 km^2) of a single gazelle was more than eight times larger than the smallest (6,431 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 km^2 for one or from 12,696 to 37,447 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 km^2 (n = 12, SD = 5,502 km^2) in year 1 to 23,556 km^2 (n = 8, SD = 14,113 km^2) in year 2 and 17,602 (n = 5, SD = 5,805 km^2) in year three (Sample 1 in Figure 2). Similarly, for the 10 individuals of Sample 2, the average range was 21,500 km^2 (n = 10, SD = 7854) in year 2 and 20,637 km^2 (n = 5, SD = 7854 km^2) in year 3 (Sample 2 in Figure 2).

Lifetime ranges of individual gazelle estimated with AKDE averaged 100,800 km^2 (n = 12, SD = 45,356 km^2), ranging from 38,100 to 167,841 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 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

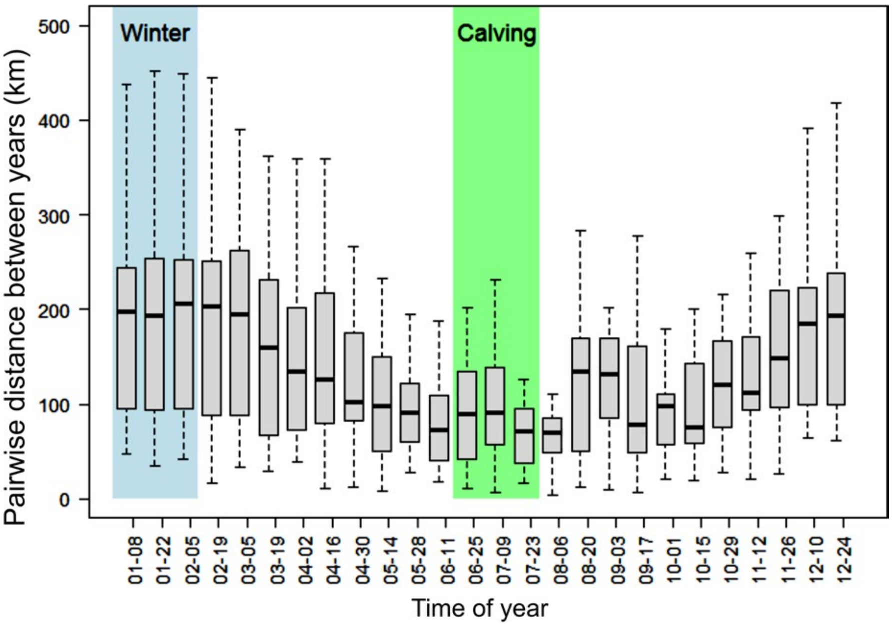

FIGURE 3 Predictability of space use between years. Each boxplot represents the distribution of pairwise distances between two 14-day mean locations of the same individual in different years. Areas used by Mongolian gazelle during wintering periods were more variable than calving periods

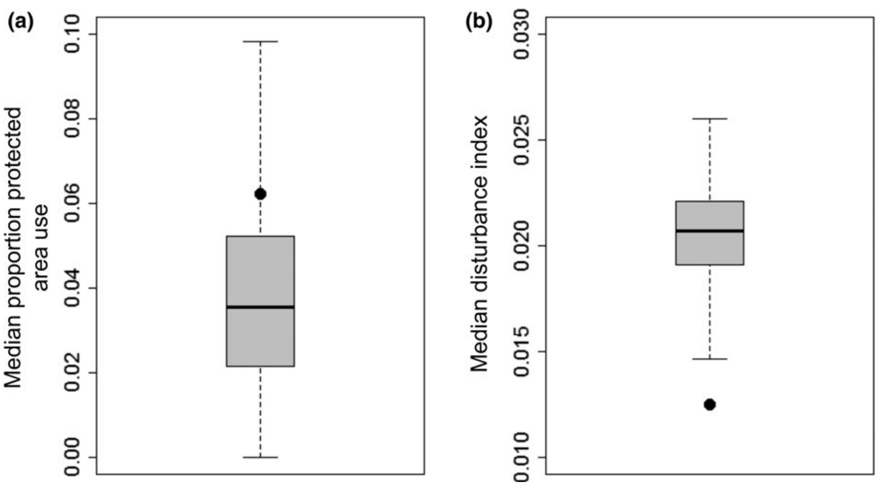

FIGURE 4 (a) A comparison of the median proportion of protected area use by tagged Mongolian gazelle (black circle) with the medians of 1,000 replicate simulations (boxplot) showed that Mongolian gazelle used protected areas similarly to random chance ($p = 0.15$). (b) A comparison of the median disturbance 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 ~19,000 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 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

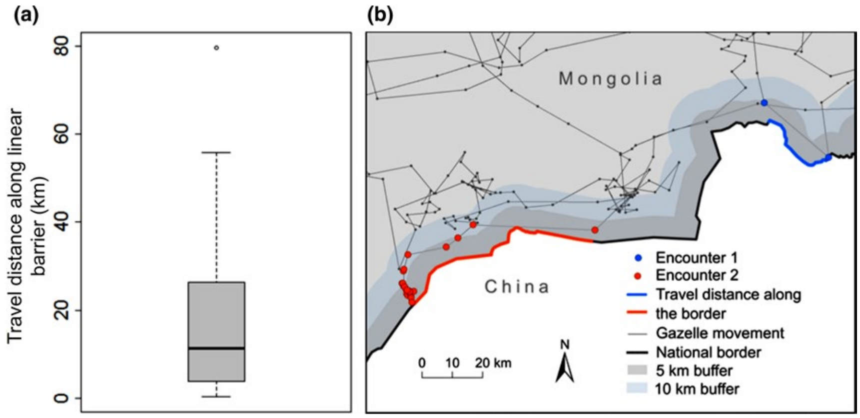

FIGURE 5 The effects of the Mongolian border fence on Mongolian gazelle movements. (a) The distribution of Mongolian gazelle travel distances along the border fence. (b) Illustration of two encounters of a single Mongolian gazelle with the border fence and their travel distances. For encounter 1 (in 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 km^2 (MCP), the estimated average lifetime range for a single gazelle was 100,800 km^2 (AKDE, Figure 2), which is half of the population core range of gazelle (~200,000 km^2; Fleming et al., 2014) and 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 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 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 km^2 suggests that the scale of conservation management must go considerably beyond the scale of existing PAs (up to 6,000 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, Victurine, 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 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 gazelle and other endangered species as well as the nomadic pastoral culture.

Where linear infrastructure cannot be rerouted to avoid conflict, we recommend that, because of the lack of fidelity in gazelle movements, crossing options should be very frequent; similar to the high density of crossing options in other successful mitigation measures for migratory ungulates (Seidler, Green, & Beckmann, 2018). On average, an individual gazelle moved 11 km along the border fences before giving up its crossing attempt. This distance might be a first minimum estimate on the necessary frequency of potential crossing options along linear barriers.

5 | CONCLUSIONS

The nomadic movements of ungulates remain largely unknown. Multiple-year monitoring data required to examine ungulates' movement characteristics in wide-open arid environments and to identify the conservation measures needed rarely exist. Incomplete knowledge about animal movements can result in inaccurate conservation assessments and ineffective management actions (Allen & Singh, 2016; Runge et al., 2014). In addition, movement studies to date rarely explore the role of these movements in shaping population abundance. Ultimately, movement data need to be coupled with robust population censuses to understand how demographic processes are linked to space use. We encourage integrated land use management policies at the landscape scale that account for landscape permeability for nomadic species wherever possible. In particular, we advocate that multiyear movement data is essential for making connectivity assessments in arid and semi-arid regions where wide-ranging nomadic species occur.

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AUTHORS' CONTRIBUTIONS

D.N. developed the ideas and methodology with contribution from T.M., C.B. and K.A.O. D.N., T.M., K.A.O. and D.M. collected the movement data. D.N. performed the analysis with contributions from T.M., C.B., J.M.C. and C.H.F. M.H. developed the disturbance index layer. T.S. completed the animation of gazelle movements. D.N. led the writing of the manuscript. All authors revised the manuscript and helped with the interpretation of results.

DATA ACCESSIBILITY

The data used in this study are available in the Dryad Digital Repository https://doi.org/10.5061/dryad.23nt63c (Nandintsetseg et al., 2019).

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SUPPORTING INFORMATION

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