1 **Nomadic ungulate movements under threat: Declining mobility of Mongolian**

2 **gazelles in the Eastern Steppe.**

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Abstract

Increasing habitat fragmentation and disturbance threaten long distance movements of ungulates. While the effects of impermeable barriers on ungulate migrations have been well researched, quantitative evidence for gradual and long-term changes of mobility in response to anthropogenic disturbance remains relatively rare.

We investigated changes in movement behavior of Mongolian gazelle *Procapra gutturosa*, a nomadic ungulate species native to the Mongolian steppe. Using GPS tracking data collected from 62 gazelle individuals between 2007 and 2021, we quantified 16-day displacement distances for each individual as a metric for long-distance movements. We used generalized linear mixed models, generalized additive models and additive quantile mixed models to assess how anthropogenic and environmental factors affected gazelle movement behavior.

Long distance 16-day movements decreased significantly by up to 36 %, from 142 km in 2007 to 92 km in 2021. Changes in gazelle mobility were affected by the increasing number of vehicles in Mongolia, but could not be explained by concurrent changes in other environmental factors like temperature, precipitation or vegetation greenness that often drive ungulate migration behavior. Moreover, we found that gazelle movement decreased close to roads, and that gazelles stayed further away from roads during the snow-free season, when vehicular traffic likely is most intense.

Conserving landscape permeability is essential for maintaining populations of highly mobile species. Our study provides evidence for a gradual decline in gazelle mobility over fifteen years as a response to increasing anthropogenic impact. To date, the transportation infrastructure permeating the Eastern Steppe does not pose physical barriers, yet our findings suggest that increasing traffic volume may create semipermeable barriers to gazelle movement. As human activity is increasing throughout the Eastern Steppe, interactions between ungulates and vehicle traffic need to be closely monitored in order to identify, localize, and mitigate semipermeable barrier effects before landscape permeability is severely altered.

Introduction

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48 The movements of land mammals are diminishing worldwide due to anthropogenic disturbances that

49 change animal behavior (Tucker et al., 2018). This effect is apparent across many taxa, influencing

50 species directly and cascading through ecosystems as critical services provided by animal movements

51 (e.g., seed dispersal) decline (Løvschal et al., 2017; Lundberg & Moberg, 2003). Among the world's

52 mammal species, ungulates are particularly affected due to their widespread reliance on long-distance-

53 movement such as seasonal migrations, which enable them to access vital resources (Fynn &

54 Bonyongo, 2011; Merkle et al., 2016) and to escape from unfavorable environmental conditions

55 (Folstad et al., 1991; Monteith et al., 2011). Consequentially, far-ranging ungulate species, such as

56 wildebeest (*Connochaetes taurinus*), bison (*Bison bison*), or saiga antelope (*Saiga tatarica*) have

57 become increasingly threatened due to the development of anthropogenic barriers, habitat loss, and

58 overhunting (Berger, 2004; Bolger et al., 2008). Mobility constraints caused by impermeable barriers

59 are perhaps the most direct threat to long distance ungulate mobility (Harris et al., 2009; Sawyer et

60 al., 2013). Where long distance movements are no longer possible, the abundance of migratory

61 ungulate species often declines drastically, as has been observed in the past (Harris et al., 2009) and

62 predicted for the future (Fryxell et al., 2004; Holdo et al., 2011). Even barriers that are not completely

63 impermeable have the potential to change movement behaviors, thereby reducing the benefits of

64 migration (Aikens et al., 2022; Sawyer et al., 2013). For such barriers, the degree of permeability may

65 vary depending on the level of human activity, and mobility may become severely impeded once

66 certain disturbance thresholds are crossed (Sawyer et al., 2020).

67 Longitudinal studies documenting the continuous and long-term decline of long-range movements are

68 rare. Much of the existing research on reductions of ungulate mobility through anthropogenic barriers

69 focused on changes in population abundance (Harris et al., 2009), spatial comparisons of mobility

70 between affected and unaffected populations (Lendrum et al., 2012) or relied on modelling (Holdo et

71 al., 2011). Some attempts at longitudinal studies have leveraged multi-year GPS data to investigate

72   effects of impermeable barriers (Ito et al., 2013), avoidance of disturbed areas (Sawyer et al., 2020) or

73   increased migration speed when moving though disturbed area (Sawyer et al., 2013).

74   We studied the effect of anthropogenic disturbance on the mobility of nomadic Mongolian gazelle

75   *Procapra gutturosa* over the course of 15 years. Mongolian gazelles (hereafter gazelles) are far-ranging

76   nomadic ungulates that primarily occur in the Gobi-Steppe ecosystem of Mongolia (Clark et al., 2006).

77   They are iconic for their vast aggregations and long distance movements in what is considered the

78   largest intact temperate steppe ecosystem worldwide (Batsaikhan et al., 2014). Previous research

79   shows that individual gazelle are capable of roaming through up to 23,000 km^2 per year, forming

80   lifetime ranges of more than 100,000 km² (Nandintsetseg et al., 2019). This high mobility is crucial for

81   the survival of gazelle, as areas of high-quality grasses and forbs occur dynamically in space and time

82   (Mueller et al., 2008). As a result, the movements of gazelle appear to be highly irregular and

83   unpredictable, with no strong fidelity to particular calving or winter ranges, no consistent migratory

84   routes, and huge temporary aggregations of individuals in times of resource scarcity (Olson et al., 2009,

85   2010).

86   Mongolia is currently experiencing dramatic socioeconomic transformations and rapid economic

87   growth as it is exploiting previously untapped, rich mineral and fossil fuel deposits (Batsaikhan et al.,

88   2014; Reading et al., 2006). These societal shifts are accompanied by the expansion of linear

89   infrastructure networks throughout the steppe (Batsaikhan et al., 2014). Our study focuses on gazelles

90   moving in Eastern Steppe within the Dornod and Sukhbaatar provinces, which represent an important

91   stronghold of the species' population. Here, road infrastructure is comprised of unfenced paved and

92   dirt roads that do not pose much of a physical barrier to ungulate movement, but create extended

93   corridors of degraded vegetation and human disturbance (Keshkamat et al., 2013). However,

94   motorized traffic in the region has been steadily increasing (National Center for Road Transport, 2022).

95   In such an environment, road infrastructure may be semi-permeable to ungulate movement, and

96   barrier effects may increase with increasing human activity (Jacobson et al., 2016; Sawyer et al., 2013).

97   Our aim was to investigate whether the mobility of gazelle in the Eastern Steppe had changed over the

98   last 1.5 decades, and if so, whether such change could be attributed to anthropogenic disturbance.

99   We analyzed changes in gazelle displacement distances over 15 years. We assessed displacement over

100   long timescales (average 16-day displacement and the 90% quantile of 16-day displacement) as human

101   disturbance may alter movement tortuosity rather than speed (Tucker et al., 2018), and encounter

102   effects could be cumulative (Eftestøl et al., 2021). To identify potential drivers of longitudinal changes

103   in gazelle movement, we assessed whether changes in vehicle numbers in Mongolia (a proxy for traffic)

104   affected gazelle mobility, while accounting for the effect of environmental drivers such as

105   temperature, precipitation, snow cover, and vegetation greenness, which have been shown to greatly

106   influence ungulate migration (Holdo et al., 2009; Laforge et al., 2021; Mason et al., 2014; Merkle et al.,

107   2016). We could not directly test for effects of traffic volume and road development since longitudinal

108   data on traffic and road construction in the Eastern Steppe were not available. We hypothesized that

109   increases in traffic and road construction change landscape permeability in the Eastern Steppe,

110   thereby reducing long-distance mobility of gazelles. Because traffic is generally lower in winter and

111   gazelle may be more tolerant of anthropogenic structures during this season (Ito et al., 2013), we also

112   hypothesized that long-term mobility declines are more apparent in summer. To corroborate effects

113   of road infrastructure on gazelle mobility, we tested whether gazelle displacement distances

114   decreased near roads using static spatial data of those features. We also tested whether gazelle

115   approached roads closer in winter than in summer, and whether this might be more apparent in gazelle

116   that stayed generally closer to human disturbance compared to gazelle that stayed farther away

117   overall.

118

Methods

Movement data of gazelle

We compiled existing GPS movement data originating from capture and collaring efforts between 2007 and 2021. All captures followed the standard protocols approved by the Ministry of Environment and Green Development in Mongolia (see details in D. Nandintsetseg et al., 2019; Olson et al., 2014). This data set included tracking data of 62 gazelle individuals with varying fix rates (see appendix A1 for details). Across these fix rates, the best feasible interval for the joint analysis of gazelle displacements (the straight-line distances between observations) over long timescales was 16-day intervals. We performed all analyses using R (R Core Team, 2021).
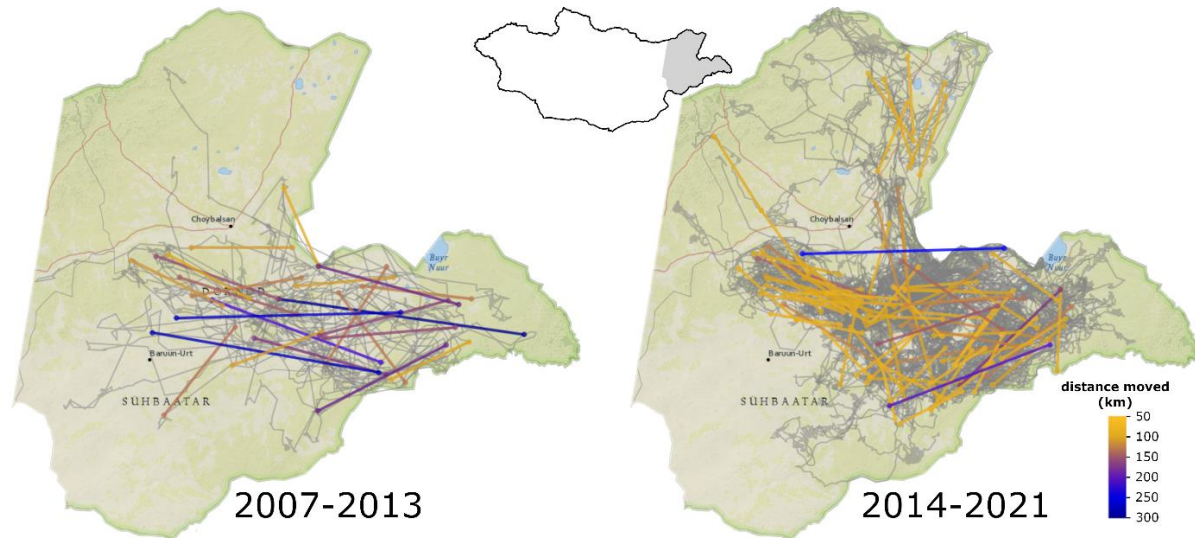
Environmental and human disturbance data

We obtained environmental covariates from the Land Processes Distributed Active Archive Center (LPDAAC), extracting monthly temperature, snow cover, and normalized difference vegetation index (NDVI) data for the years 2007 - 2021, obtained at 0.05-degree resolution by Terra MODIS (Didan, 2015; Hall & Riggs, 2015; Wan et al., 2015). From the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) data archive (Funk et al., 2014), we acquired monthly precipitation data for the same time periods, also at 0.05-degree resolution.

We acquired yearly data on the number of registered vehicles in Mongolia between 2012 and 2021 (National Center for Road Transport, 2022). Data on registered vehicles in 2007-2011 were not available, however we obtained data on the number of imported vehicles during that time and used them to calculate the number of vehicles in Mongolia in that period (assuming that imported vehicles were registered in the year of import, and that no vehicles were produced in Mongolia). To measure the proximity of gazelles to road infrastructure we accessed road maps from the Administration of Land Affairs, Geodesy, and Cartography of Mongolia (ALAGaC, Agency of Land Administration and Management Geodesy and Cartography Mongolia, 2022) and from OpenStreetMap (OpenStreetMap

143   Contributors, 2022). These spatial data provide a snapshot of the current distribution of disturbances

144   throughout the steppe.

145   For each displacement step, we calculated mean temperature, precipitation, snow cover and NDVI, as

146   well as the mean distance to the nearest road. We also recorded the year, month, and coordinates of

147   the first position in each step, as well as the unique identifier for each individual gazelle. We classified

148   each step into a snow-free season (April – October) or winter season (November – March). To assess

149   long distance displacements, we determined whether any step belonged to the 10% of longest steps

150   moved during each season per year, over all gazelles.

151

152   **Figure 1: Gazelle long-distance displacements in summer** as straight line 16-day distances, on top of

153   actual gazelle movement paths (in grey). The background depicts the Dornod and Sukhbaatar

154   provinces of Mongolia. This map was created via the R package `leaflet`, background tiles © Esri –

155   National Geographic, Esri, DeLorme, NAVTEQ, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO,

156   NOAA, iPC.

157   **Assessing longitudinal effects on displacement**

158   We assessed the effect of year on gazelle displacement by building linear mixed models for the winter

159   and snow-free seasons, using displacement distance as the response variable and year as the only

160   predictor. To determine whether long distance movement was especially affected, we repeated the

161   analysis using only the longest 10% of displacement steps. To assess potential anthropogenic drivers,

162   i.e., the effect of increasing human activity while correcting for potential environmental changes, we

163   built a second set of linear mixed modes using the number of vehicles (in hundred thousand),

164   temperature (in °C), NDVI, precipitation (in mm), and snow cover (in %) as predictors. Models for the

165   snow-free season did not incorporate snow cover. All models included a random intercept for gazelle

166   individual to account for interindividual differences.

167   We computed Cullen and Frey graphs via the `fitdistrplus` package (Delignette-Muller & Dutang,

168   2015) to identify suitable transformations of the response variables, after which we cube-root

169   transformed displacement in all models. We tested whether including a quadratic term of NDVI

170   improved the predictive power of the model as measured by Akaike's Information criterion (AIC;

171   Akaike, 1974), as gazelles might prefer intermediate values of NDVI (Mueller et al., 2008). Subsequently

172   we added a quadratic term for NDVI in all models that incorporated NDVI. We tested for correlation

173   between predictor variables by calculating pairwise Pearson correlation coefficients. Temperature and

174   snow cover were always highly correlated ($\rho > |0.6|$), so we included one of these parameters at a

175   time and calculated the AIC to determine the parameter with the highest predictive power, and

176   consequently kept temperature in the model while discarding snow cover (see appendix A2).

177   We assessed model assumptions using the `DHARMa` package (Hartig, 2021) (see appendix A3). In the

178   presence of influential outliers or heteroscedasticity, we refitted the respective models as robust linear

179   mixed effect models using the rlmer function in the `robustlmm` package (Koller, 2016). Because rlmer

180   does not compute p-values, we used the t-statistics of the "robust" rlmer model together with the

181   Satterthwaite degrees of freedom of the "normal" lmer model to determine significance (see e.g.

182   Geniole et al., 2019; Gómez et al., 2022). We tested for the presence of spatial autocorrelation (SAC)

183   in the model residuals using the test for Moran's I in the `ape` package (Paradis & Schliep, 2019). In

184   case we detected significant SAC, we employed Moran's eigenvector maps following Bauman et al.

185   (2018) to reduce SAC (see appendix A4). We calculated the partial R^2 attributed to each model

186   covariate using the `partR2` package (Stoffel et al., 2021) and computed back-transformed predicted

187   marginal means with 0.95 confidence intervals for each predictor using the `ggeffects` package

188   (Lüdecke, 2018) and the `emmeans` package (Lenth, 2021). Finally, we refitted all models without using

189   variable transformations, robust models or autocorrelation corrections to ensure that significant

190   trends did not arise as artifacts of those additions (see appendix A5).

191   **Assessing the effect of anthropogenic disturbance on displacement**

192   We modelled the effect of proximity to roads on average 16-day gazelle displacement via generalized

193   additive models, using the `mgcv` package (Wood, 2011). We employed a Gaussian Location-Scale

194   Model via the "gaulss" family to achieve unbiased p-values in the presence of heteroscedasticity. As in

195   the previous analyses, we cube-root transformed the response to achieve normally distributed

196   residuals. Predictors included thin plate regression splines of the mean and standard deviation of the

197   distance to the nearest road as well as random intercepts for gazelle individuals and years. We

198   assessed spatial dependence in the model residuals as described previously and accounted for it by

199   including a smoothed interaction term of the spatial coordinates at the start of each displacement

200   step. We also tested whether an interaction between distance to road and season improved model fit

201   using AIC (see appendix A6). Additionally, we $\log_{10}$-transformed the distance to roads as we were most

202   interested to model potential effects close to the source of disturbance. Because roads might often be

203   located close to other sources of human disturbance, we excluded displacement steps during which

204   gazelles were observed within 10 km of a settlement, railway or oil extraction site from this analysis

205   (353 of 1903 data points), using railway maps digitized from google earth imagery (Google Earth, 2022)

206   and spatial data on the location of settlements and oil wells from ALAGaC (Agency of Land

207   Administration and Management Geodesy and Cartography, 2022) and the environmental department

208   of Dornod province (Department for Environment of Dornod Aimag, 2015).

209   **Assessing seasonal effects of disturbance**

210   To test the effect of season on the proximity of gazelles to roads, we calculated the average distance

211   of each gazelle to the nearest road during both the snow-free and winter season of each year. We
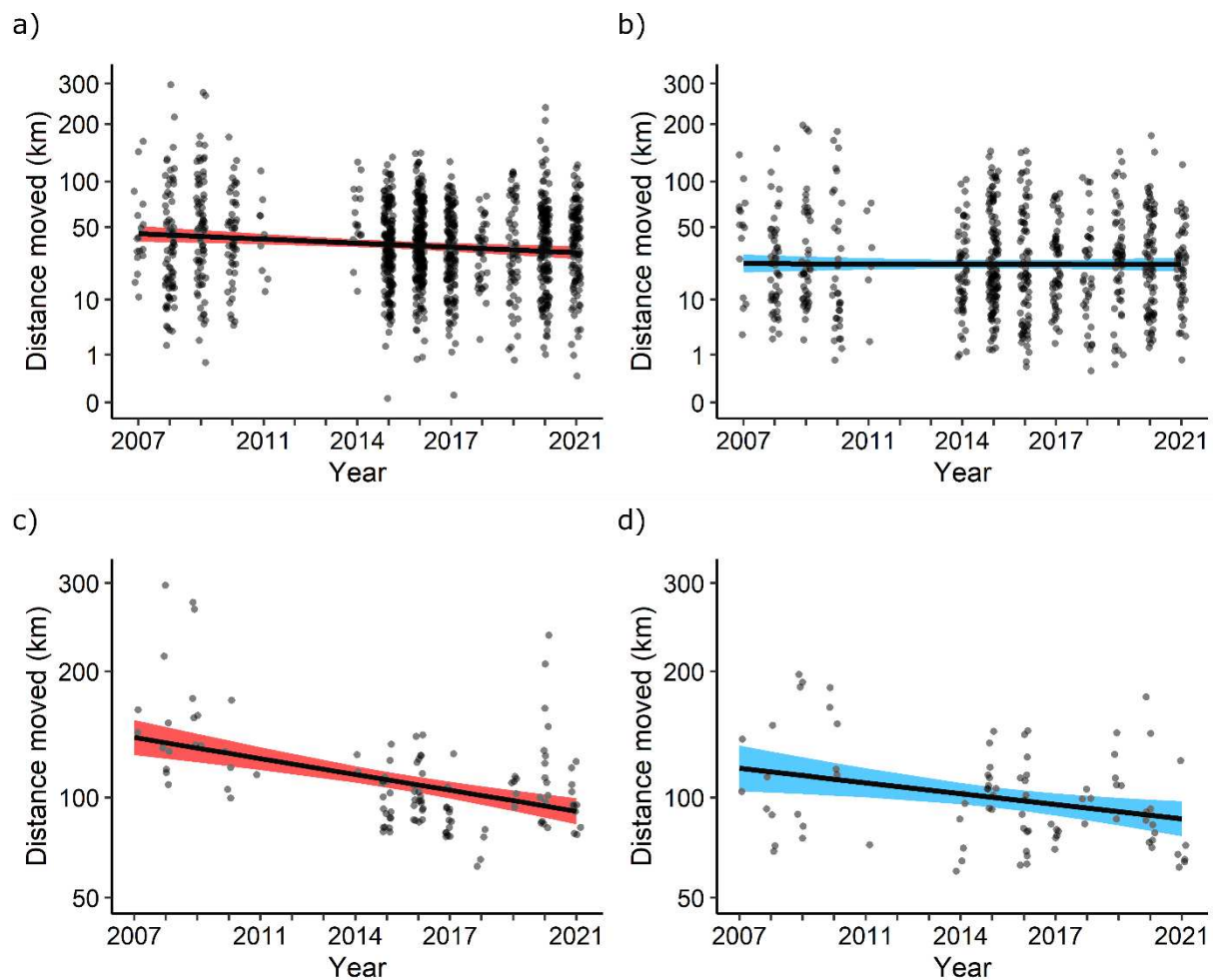
212   tested the effect of season and year on the 0.1, 0.25, 0.5, 0.75 and 0.90 quantile of distances to roads

213   in an additive quantile mixed model framework using the `aqmm` package (Geraci, 2019), including a

214   random intercept to account for differences between individuals. Additive quantile mixed models

215   produce robust results in the presence of non-normally distributed or heteroscedastic errors (Geraci,

216   2019; Yirga et al., 2021).

217

Results

Longitudinal effects on gazelle displacement

Over the 15-year study period, we detected a significant decrease in average gazelle movements at 16-day intervals during the snow-free season (β = -0.028, t = -3.025, p = 0.004), but not during winter (β = -0.001, t = -0.132, p = 0.895). During the snow-free season, the estimated marginal mean of 16-day displacement decreased from 44.4 km [0.95 ci: 38.6; 51.1] in 2007 to 31.3 km [27.3; 35.3] in 2021, constituting a decline by 29.5 % (13.1 km) over 15 years (Figure 2a). When including only the longest 10% of gazelle movements per year, we detected significant longitudinal decreases during both the snow-free (β = -0.050, t = -5.602, p < 0.001) and winter seasons (β = -0.034, t = -2.889, p = 0.006). In the snow-free period, the estimated marginal means of 16-day long distance displacement decreased from 142.2 km [128.8; 155.7] in 2007 to 91.7 km [84.6; 99.9] in 2021, constituting a decrease by 35.5 % (50.5 km) over 15 years (Figure 2c). In winter, the estimated marginal means of 16-day long distance displacement decreased from 119.1 km [103.8; 135.8] in 2007 to 87.5 km [77.9; 98.0] in 2021, decreasing by 26.5 % (31.6 km) (Figure 2d).
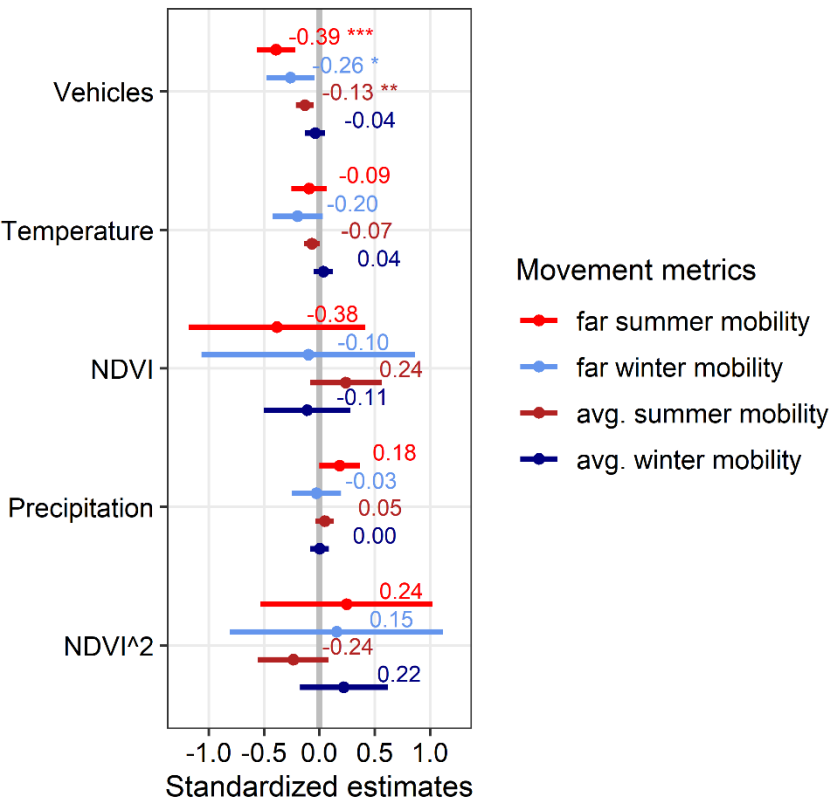
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Figure 2: Effect of year on average and long-distance gazelle displacements. The predicted marginal means of the effect of year on the back-transformed average (a, b) and long-distance (c, d) 16-day displacements during the snow-free (a, c) and winter seasons (b, d) are depicted with 95% confidence bands. Average displacements decreased strongly over time during the snow-free season, while long-distance displacements decreased strongly during both seasons.

Potential drivers of declines in mobility

The increasing number of vehicles in Mongolia negatively affected average gazelle mobility in the snow-free season (β = -0.050, t = -3.254, p = 0.002), and long-distance mobility of gazelles in both the snow-free (β = -0.078, t = -4.461, p < 0.001) and winter season (β = -0.049, t = -2.358, p = 0.024), while accounting for concurrent changes in environmental factors and inter-individual differences. Only average winter mobility was not significantly affected by number of vehicles (Figure 3). During the

244 study period, the number of vehicles in Mongolia increased by 373.6 %, from 301,195 vehicles in 2007

245 to 1,125,385 vehicles in 2021. Concurrently, the estimated marginal means of average gazelle mobility

246 decreased from 45.9 km [39.7; 52.7] to 31.9 km [27.5; 36.3] during the snow-free season, constituting

247 a decrease of 14.0 km (30.6 %). For long-distance mobility, the estimated marginal means decreased

248 from 136.6 km [120.6; 154.0] to 91.1 km [82.9; 100.5] during the snow-free season, constituting a

249 decrease of 45.5 km (33.3 %); and from 113.4 km [98.6; 129.6] to 86.9 km [76.8; 98.0] during winter,

250 constituting a decrease of 26.4 km (23.3 %). Temperature, NDVI, and precipitation did not significantly

251 affect gazelle displacement in any model (Figure 3). The snow-free model explained 4.6 % of the

252 variation in average gazelle displacement, with 1.2 % attributed to the vehicle effect. For long-distance

253 mobility, the snow-free model explained 25.8 % of the variation in average gazelle displacement, with

254 16.8 % attributed to the vehicle effect; whereas the winter model explained 13.7 %, with 7.4 %

255 attributed to the vehicle effect. See appendix A5 for model summary tables.
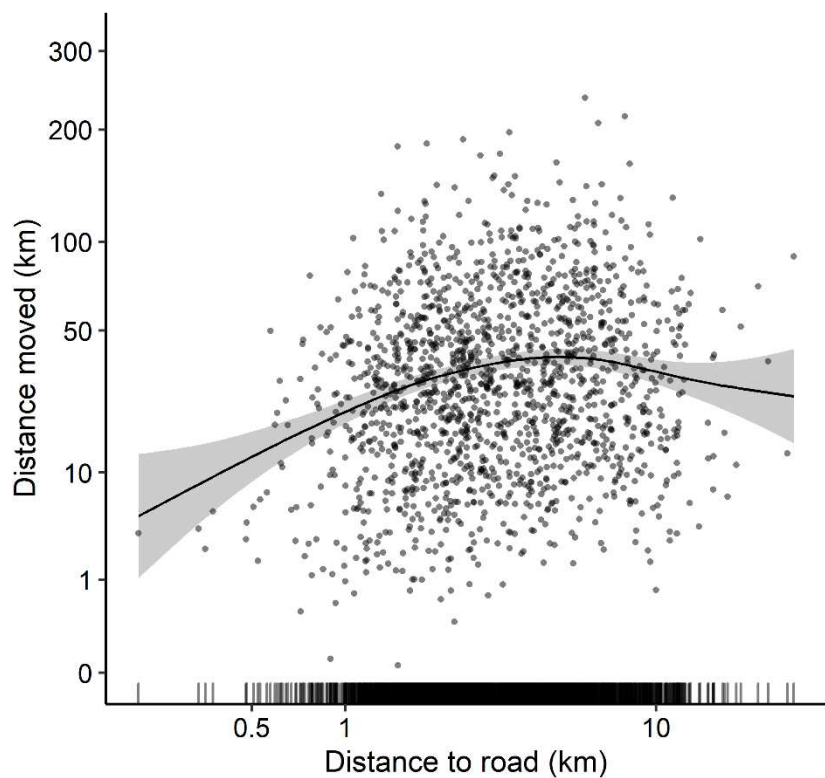
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Figure 3: Standardized estimates of potential drivers of gazelle mobility for all constructed models.

Vehicle number significantly affected gazelle mobility in all models except for average winter mobility, while no other predictor affected mobility. Standardized effect sizes were higher during the snow free season and for long-distance movement, compared to the winter season and average movement.

Effects of road infrastructure on movement

The average distance to the nearest road significantly affected gazelle displacement (edf = 3.676, Chi.sq = 73.291, p < 0.001), while controlling for differences between individuals and years. Gazelle movements decreased in close proximity to roads, averaging 43.6 km [32.7; 58.1] at 10 km from the nearest road, but only 27.1 km [20.9; 35.1] while on average 1 km from it (Figure 4). The model explained 15.8 % of the residual deviance (10.6 % when excluding distance to road). There was no support for an interaction between distance to road and season. See appendix A5 for model summary tables.
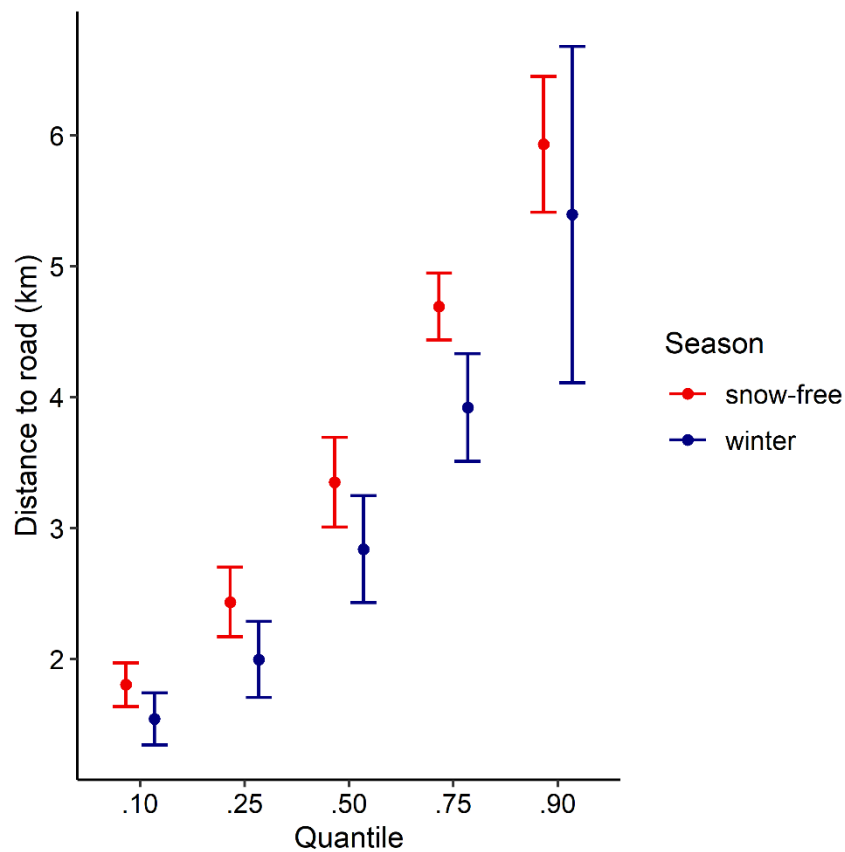
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Figure 4: GAM response curve of the effect of distance to roads on 16-day displacement distances.
Axis values are back-transformed to kilometers. Displacement distances decreased close to roads but
stayed relatively constant once gazelles were several kilometers away from it.

Seasonal differences of disturbance effects

Season significantly affected the 0.1, 0.25, 0.5 and 0.75 quantile of gazelle distances to roads. In winter,
the estimated median distance to roads was 512.2 m (SE = 207.9, t = -2.463, p = 0.016) closer than the
snow-free estimate of 3352 m, constituting a decrease of 15.3 % (Figure 5). The estimated 0.1 quantile
of distances decreased by 261.4 m (SE = 101.2, t value = -2.584, p = 0.011) compared to the snow-free
estimate of 1805.4 m (14.5 %), while the estimated 0.25 quantile of distances decreased by 438.6 m
(SE = 148.2, t value = -2.960, p = 0.004) compared to the snow-free estimate of 2436.4 m (18 %). The
0.75 quantile of distances decreased by 770.7 m (SE = 210, t value = -3.670, p < 0.001) compared to
the snow-free estimate of 4683 m (16.4 %). Year did not affect distances to roads in any quantile. See
appendix A5 for model summary tables.

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Figure 5: Seasonal differences in the distance of gazelles to the nearest road for multiple quantiles, with 95% confidence intervals. Most gazelles moved significantly closer to roads in winter, only gazelles that stayed very far from such disturbances did not.

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Discussion

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291   We identified a decline of up to 13.1 km (29.5%) in the average and up to 50.5 km (35.5%) in the long-

292   range movement behavior of gazelle covering a period of 15 years in a context of increasing

293   anthropogenic disturbance. Decreases in gazelle mobility were correlated with the increasing number

294   of vehicles and the presence of roads. Declines were more pronounced during the snow-free period,

295   and gazelles displayed an increased avoidance of roads during that time. Our findings suggest that

296   gazelle mobility in the Eastern Steppe decreased in response to human disturbance, potentially due to

297   increases in road development and traffic.

298   Our study may be among the first to quantify gradual declines in ungulate movement distances over

299   time. Decreases in ungulate migration have frequently been observed following the construction of

300   anthropogenic barriers, which have affected migration propensity and migration routes in many

301   ungulate populations, often culminating in the complete cessation of migratory behavior (Harris et al.,

302   2009; Xu et al., 2021). Past research has collated quantitative evidence for the loss of ranges (Holdo et

303   al., 2011; Said et al., 2016), routes (Berger, 2004) and abundances of migratory ungulate populations

304   in response to anthropogenic development (Bolger et al., 2008; Holdo et al., 2011; Said et al., 2016).

305   Previous research has also compared current and historic records of ungulate migration distances

306   (Harris et al. 2009) and found that mammal movements decreased in areas of high human footprint

307   using a space-for-time approach (Tucker et al. 2018). However, long-term individual-based data sets

308   remain scarce but are urgently needed to determine how anthropogenic effects change ungulate

309   behavior over time (Kauffman et al., 2021; Xu et al., 2021). Gradual effects of anthropogenic barriers

310   have been observed in migratory mule deer (*Odocoileus hemionus*) where the increasing intensity and

311   size of energy development caused detours in migration routes and affected migration timing (Aikens

312   et al., 2022; Sawyer et al., 2013, 2017).

313

Traffic and transportation infrastructure may affect gazelle mobility

Gazelles in our study may have responded to increases in traffic volume creating a disturbance barrier, rather than to a physical barrier created by roads. Contrary to many European or North American study systems, roads in the Eastern Steppe usually are dirt roads that likely do not pose impermeable physical barriers (Keshkamat et al., 2013; Yang et al., 2018). In addition, vehicle traffic has been observed to induce road avoidance behaviors in a wide range of species through disturbance cues such as noise or movement (Fahrig & Rytwinski, 2009; Jaeger et al., 2005), creating semi-permeable barriers whose effect could be mediated by the level of disturbance (Alexander et al., 2005; Sawyer et al., 2013). Such effects have also been observed near unpaved roads with low traffic volumes (D'Amico et al., 2016). Ungulate species known to avoid roads specifically due to vehicle traffic include red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) (Gagnon et al., 2007; Thurfjell et al., 2015), while others like pronghorn and Tibetan antelope (*Pantholops hodgsonii*) displayed increased vigilance behavior at high levels of traffic, suggesting they perceived cars as a threat (Gavin & Komers, 2007; Lian et al., 2011). Vehicle avoidance in gazelle may be exacerbated by the frequent use of cars and motorcycles for hunting. The plain landscape of the steppe makes wildlife easily accessible by vehicle, and both legal and illegal hunting frequently occur (Olson et al., 2014). During soviet times, gazelles were commercially hunted in large numbers, sometimes using trucks and automatic weapons (Lhagvasuren & Milner-Gulland, 1997). We observed gazelles to be shy to cars, initiating flight responses if a single car passed by them at several hundred meters distance and low speed (pers. comm. N. Dejid), although in some other regions to the south-west outside our study area gazelles may already show signs of habituation to cars where traffic volumes are high but hunting is less frequent (pers. comm. K. Olson). Hunting also affected road interactions in moose, increasing road avoidance during hunting season and in individuals that experience high hunting pressure (Paton et al., 2017). Road effects are known to be more severe for far-moving species because they encounter linear features frequently (Fahrig & Rytwinski, 2009; Jakes et al., 2018), which may also explain why our proxy for traffic explained much more variation in long-distance movement than in average movement.

Seasonal differences in gazelle reactions to anthropogenic disturbance

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341   We observed that declines in average and long-distance mobility were less strong in winter than during

342   the rest of the year, while gazelles also stayed closer to roads in winter. This reduced avoidance of

343   anthropogenic infrastructure during winter is consistent with findings of Kaczensky et al. (2006) and

344   Ito et al. (2013), who reported that both gazelle and Asiatic Wild Ass (*Equus hemionus*) moved closer

345   to anthropogenic barriers during that time. If the observed reductions in gazelle mobility are caused

346   by traffic, the decreased human activity during the harsh Mongolian winter could explain why

347   reductions of gazelle mobility were less pronounced during that time. Alternatively, the need to escape

348   inhospitable environmental conditions such as snowstorms, deep snow cover, or lack of forage could

349   have temporarily outweighed the avoidance of anthropogenic features in gazelle during winter. In

350   other ungulates, pronghorn and mule deer avoided anthropogenic disturbance in winter, but tolerance

351   for anthropogenic disturbance increased during migration; i.e. when there was a need to move

352   through disturbed area (Sandoval Lambert et al., 2022).

Consequences of decreasing mobility for nomadic ungulates

353

354   Decreased locomotion capacity can have drastic consequences for population levels of ungulates

355   (Harris et al., 2009), causing events of high mortality in many migratory populations due to lacking

356   access to vital resources (Williamson et al., 1988). Nomadic ungulate populations, such as gazelle, may

357   be more resilient to anthropogenic impacts than migratory populations due to their high plasticity in

358   route and sites use, yet they are also difficult to protect due to their far-ranging movements

359   (Nandintsetseg et al., 2019), and many nomadic species are in decline (Runge et al., 2014). Nomadism

360   represents an adaptation to environments where resource availability is low and highly variable in

361   space and time. The survival of nomadic populations may depend on their ability to access dynamically

362   changing resources by displaying long-range movement throughout the year (Mueller et al., 2008).

363   Hence, constraining their ability to move far could greatly impact the abundances of nomadic

364   populations. In Mongolia, the construction of the Trans-Mongolian railway in the 1950s was followed

365   by drastic population declines of gazelles to the west of the railway when their habitat was bisected

366   (Lhagvasuren & Milner-Gulland, 1997). Similarly, the winter mortality of spatially confined Przewalski

367   horses (*Equus ferus przewalskii*) was observed to be higher than in more mobile Asiatic wild ass

368   (Kaczensky et al., 2011). Population densities of Thompson's gazelle (*Eudorcas thomsonii*) in Kenya,

369   another ungulate considered to be nomadic (Fryxell et al., 2004), decreased following the construction

370   of fences, although decreases in migratory wildebeest and impala in the same area were more

371   dramatic (Said et al., 2016). Partially nomadic pronghorn in North America displayed behavioral

372   avoidance close to wind turbines and reduced habitat use near roads, albeit without immediate

373   negative effects (Milligan et al., 2021).

374   **Alternative explanations for the decrease in mobility**

375   Many ungulate species adjust their mobility patterns in response to environmental conditions,

376   especially forage availability (Bartlam-Brooks et al., 2013; Merkle et al., 2016), and migration distances

377   often decrease with increasing NDVI (Teitelbaum et al., 2015). Nomadic ungulates exhibit high mobility

378   driven by the scattered and irregular occurrence of resources (Dejid et al., 2019; Mueller et al., 2008),

379   and a decrease in mobility could indicate changes in the overall pattern of forage in space and time.

380   Vegetation greenness in the Eastern Steppe has increased during the last decades (Meng et al., 2020),

381   and a recent climate risk assessment of Mongolia reported that both temperatures and precipitation

382   are predicted to increase under most emission scenarios (World Bank Group & Asian Development

383   Bank, 2021), potentially increasing vegetation productivity, and hence forage availability. In this

384   scenario, the need for continual long-distance mobility could be partially alleviated. Although we found

385   no effect of local NDVI on gazelle displacement, we cannot completely rule out that improving forage

386   conditions might have contributed to the observed decrease in mobility.

387   **Conservation implications for gazelle in the Eastern Steppe**

388   Maintaining large-scale landscape permeability is critical to conserving wide-ranging ungulates such as

389   gazelle (Nandintsetseg et al., 2019). However, impermeable fences along the Trans-Mongolian

390   Railroad and the Mongolian-Chinese border are already impacting gazelle (Ito et al., 2013;

391   Nandintsetseg et al., 2019), and the proposed construction of additional railroads throughout the

392   Eastern Steppe will likely exacerbate this issue (Batsaikhan et al., 2014). Our findings add an additional

393   perspective to this already concerning outlook: landscape permeability in the Eastern Steppe may be

394   further impacted by increasing traffic intensity, creating semi-permeable barriers to movement. Such

395   barriers have been associated with population declines e.g. in migratory mule deer (Sawyer et al.,

396   2017). Currently, we lack the data to assess whether the decline of gazelle mobility has impacted

397   gazelle population sizes in the Eastern Steppe, as assessments of gazelle abundance have been

398   infrequent and vary in methods and range, with the last published survey likely preceding the onset of

399   potential traffic effects (Olson et al., 2005). Traffic volumes in the sparsely populated Eastern Steppes

400   likely are still far from the level observed in other systems. The decrease in gazelle mobility estimated

401   by our models is relatively low compared to the findings of Tucker et al. (2018), who reported that

402   mammal movements decreased by factor 2-3 in areas of high human footprint. Yet, even if no drastic

403   effects are visible to date, the impact of semi-permeable barriers might change drastically once certain

404   permeability thresholds are reached (Sawyer et al., 2013). The number of registered vehicles in the

405   Eastern Steppe is already consistently increasing (National Center for Road Transport, 2022),

406   suggesting that both traffic and traffic-mediated barrier effects may only grow in intensity.

407   In its vision for long-term development, the Government of Mongolia has declared to create the

408   transportation infrastructure necessary for an export-oriented economy, and to connect all its

409   settlements with roads until 2050 (State Great Hural, 2020). However, this ambitious goal conflicts

410   with the country's vision to protect biodiversity and maintain ecosystem services. It also comes at the

411   risk of losing the county's great herds of nomadic ungulates, which not only provide benefits for

412   regional ecotourism and subsistence hunting, but also serve as a symbol for a vast and undisturbed

413   ecosystem whose people themselves are deeply rooted in their nomadic traditions. To conserve

414   Mongolia's wide-ranging ungulates, it will be crucial for future infrastructure development policies and

415   land use plans to address the issue of decreasing landscape permeability. We suggest that proposed

416   land-use monitoring efforts already part of the Vision 2050 need to be extended to explicitly

417   encompass the proposed and ongoing road construction projects. To implement scientifically sound

418   policies on environmental protection, long-term assessments of gazelle mobility and abundance need

419   to be continued and supplemented with regular surveys on traffic volumes in core gazelle habitat. This

420   will enable conservationists to look past the high interannual and interindividual variability of

421   movement patterns, pre-emptively identify critical thresholds in landscape permeability and react to

422   barrier effects long before mobility has declined to the point that populations are severely affected.

423   Improving our understanding of how gazelle behaviors are affected by traffic will be crucial to develop

424   mitigation measures for declining permeability. Potentially, barrier effects posed by roads could be

425   alleviated by decreasing the risk perception of vehicles, for instance by prohibiting the use of vehicles

426   for hunting purposes.

427   **Conclusion**

428   Our study raises concerns on how increasing anthropogenic disturbance threatens large-scale ungulate

429   mobility across the world's largest mostly-intact grassland, and provides new insights on how nomadic

430   ungulates are affected by semi-permeable barriers. The Mongolian Eastern Steppe is widely known as

431   a land without fences, allowing grand accumulations of ungulates to roam freely through a largely

432   undisturbed ecosystem. However, we documented gradual declines in gazelle mobility in the Eastern

433   Steppe, potentially due to increases in vehicle traffic throughout the steppe and related disturbances

434   such as degraded vegetation around dirt roads. While the effects of this declining mobility on gazelle

435   populations are currently unknown, they may foreshadow significant declines in abundance as traffic

436   and road infrastructure continue to expand and landscape connectivity decreases. Further research

437   will be essential to pinpoint critical thresholds in barrier permeability, and to forecast when these

438   thresholds will be reached.

439

Acknowledgements

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