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Integrating GPS Telemetry and NDVI Using the Relative Route Utilization Index for the Ural Saiga Population

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ABSTRACT

Quantifying spatial use by migratory ungulates requires movement and environmental data at comparable spatial and temporal scales. We developed the Relative Route Utilization Index (RRUI) to aggregate annual route geometries when original time-stamped GPS fixes are unavailable. The study covered five districts of the West Kazakhstan Region used by the Ural saiga population (Saiga tatarica) during 2012-2024. We consolidated 184 telemetry records into 113 animal-year routes and combined district-year RRUI values with growing-season MODIS NDVI, climate variables, and livestock numbers in a balanced panel of 65 district-year observations. RRUI averaged 0.200 (SD = 0.187; range = 0.000–0.626), indicating substantial variation in the relative distribution of tracked routes among districts and years. Two-way fixed-effects models produced consistently negative RRUI coefficients across three specifications (−0.0184, -0.0163, and −0.0172). However, the RRUI–NDVI association was not statistically robust under CR2 and wild cluster bootstrap inference, which accounted for only five spatial clusters. The results therefore do not establish a robust or causal effect of saiga space use on vegetation condition. RRUI is a transparent aggregation measure for aligning annual routes with management-scale environmental data. It does not replace established movement models and should not be interpreted as a measure of population abundance, residence time, grazing damage, or movement intensity. The analysis code and computational workflow are available in an open repository.

Keywords: *Saiga antelope, GPS telemetry, Rangeland monitoring, Remote sensing, NDVI, Dryland management*

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INTRODUCTION

The saiga (Saiga tatarica) is a characteristic species of Eurasian steppe and semi-desert ecosystems and is notable for its high spatial mobility. It undertakes extensive seasonal movements in response to spatio-temporal variation in forage resources, climatic conditions, and water availability (Bekenov *et al*., 1998; Milner-Gulland *et al*., 2003; Kauffman *et al*., 2021a; Abraham *et al*., 2022). Saiga populations in Kazakhstan have recovered substantially in recent years, with particularly pronounced growth in the Ural population (Serikbayeva *et al*., 2023). Nevertheless, saiga remain vulnerable to mass mortality associated with weather anomalies (Kock *et al*., 2018). We focused on the Ural population because of its conservation importance, high spatial mobility, and the availability of multi-year GPS-telemetry data for 2012-2024, which permit relative space use to be examined over an extended period.

The growth of the Ural population has increased its interaction with agricultural areas of West Kazakhstan, where saiga and domestic livestock use shared rangeland landscapes (Khanyari *et al*., 2022; Koshkina *et al*., 2026). Expansion of linear transport infrastructure may also affect habitat accessibility and the spatial connectivity of saiga migration routes (Bizhanova *et al*., 2025). Linear features and industrial development can constrain ungulate movement or decouple it from vegetation gradients (Passoni *et al*., 2021; Aikens *et al*., 2022; Jones *et al*., 2022). These conditions increase the need to quantitatively assess saiga space use and its temporal variation.

Advances in GPS telemetry have substantially expanded opportunities to study the spatial ecology of migratory animals (Cagnacci *et al*., 2010; Hebblewhite & Haydon, 2010; Tomkiewicz *et al*., 2010). GPS data support analysis of individual trajectories, seasonal movements, and changes in space use in relation to environmental conditions. Contemporary movement ecology (Nathan *et al*., 2008; Morelle *et al*., 2015) includes the concept of resource tracking, whereby animals alter spatial behavior in response to spatio-temporal dynamics in resource availability (Merkle *et al*., 2016; Aikens *et*

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al., 2020; Abrahms *et al*., 2021; Kauffman *et al*., 2021a). Previous saiga studies have linked seasonal movements to vegetation dynamics and other environmental characteristics (Singh *et al*., 2010a, 2010b; Singh & Milner-Gulland, 2011). Many ungulate migrations nevertheless remain insufficiently mapped and protected, while GPS telemetry is increasingly used to inform conservation decisions (Kauffman *et al*., 2021b).

In parallel, satellite remote sensing enables systematic assessment of vegetation condition and its spatio-temporal variability. The Normalized Difference Vegetation Index (NDVI) is among the most widely used indicators of vegetation-cover condition and dynamics (Tucker, 1979; Pettorelli *et al*., 2005; Pettorelli, 2013). MODIS data provide long and comparable NDVI time series, including for monitoring vegetation in Central Asian rangeland ecosystems (Huete *et al*., 2002; Formica *et al*., 2017). Seasonal saiga movement has previously been related to spatio-temporal vegetation dynamics (Singh *et al*., 2010b). Combining GPS telemetry with satellite data therefore allows animal spatial behavior to be compared with changes in vegetation condition.

Land-use and land-cover change is increasingly recognized as an important spatial context for human-wildlife interactions. Expansion of settlements and agricultural land, habitat degradation, and fragmentation can reduce the availability and connectivity of natural habitats, increasing the likelihood that wildlife uses areas shared with people and livestock. Conflict risk is therefore often concentrated at landscape interfaces, including protected-area boundaries and mosaics where natural vegetation occurs alongside cultivated or built-up land. These relationships are not restricted to rapidly transformed locations; persistent interactions may also occur in relatively stable habitats where wildlife activity and human land use remain in proximity (Njomi *et al*., 2026).

Remote sensing and GIS provide a practical framework for examining these relationships across space and time. Njomi *et al*. (2026) combined multi-temporal Sentinel-2 land-use and land-cover classification with kernel density estimation and spatial overlay analysis around Hluhluwe-iMfolozi Park in South Africa. Their results showed that conflict events were concentrated near the protected-area boundary and were increasingly associated with grassland, woodland, and transitional landscapes. The study also found that land-cover change was more pronounced outside the protected area, where anthropogenic pressures were stronger. This evidence supports using harmonized spatial datasets to identify locations where vegetation change, habitat configuration, and wildlife presence overlap.

The methodological limitations Njomi *et al*. (2026) identified are also relevant to movement-based monitoring. Their analysis treated the observed patterns as spatial associations rather than causal effects because conflict records did not fully match the land-cover intervals, reporting effort may have varied, and wildlife movement was inferred from spatial patterns rather than measured directly with GPS telemetry. These constraints indicate a need for approaches that connect direct movement information with remotely sensed vegetation data at compatible spatial and temporal scales. The present study addresses this narrower data-integration problem by converting annual GPS routes into RRUI district-year values and aligning them with NDVI, climate, and livestock indicators, while retaining a non-causal interpretation of the estimated associations.

Movement ecology provides a broad set of methods for analyzing animal spatial behavior, including Kernel Density Estimation (KDE), Brownian Bridge Movement Models (BBMM), Autocorrelated Kernel Density Estimation (AKDE), Continuous-Time Movement Models (CTMM), Local Convex Hull (LoCoH), Resource Selection Functions (RSF), and Step Selection Functions (SSF). These methods estimate space use, account for the sequence and temporal structure of GPS observations, and analyse habitat selection in relation to environmental characteristics (Worton, 1989; Boyce *et al*., 2002; Manly *et al*., 2002; Getz & Wilmers, 2004; Fieberg & Kochanny, 2005; Horne *et al*., 2007; Long & Nelson, 2013; Fleming *et al*., 2015; Avgar *et al*., 2016; Calabrese *et al*., 2016).

This study uses open GPS-telemetry data for the Ural saiga population published in the Atlas of Ungulate Migration (GIUM) (Salemgareyev & Zuther, 2024). The available data comprise aggregated annual routes for individual animals, whereas the open dataset does not include the original sequences of time-stamped GPS fixes. This structure prevents direct application of methods requiring the original GPS-fix sequences and their temporal structure. A separate aggregation problem therefore arises: annual routes must be converted into a single normalized indicator of relative area use that is comparable among districts and years and compatible with environmental indicators at the same spatio-temporal scale. We address this problem by proposing the Relative Route Utilization Index (RRUI). RRUI is not an alternative to established movement models; it aggregates open annual GPS-route data at the district–year level.

Open telemetry data also require cautious interpretation. Tracked animals form a sample rather than the entire population, and spatial metrics derived from GPS telemetry may depend on the number and composition of tracked individuals (Börger *et al*., 2006). RRUI therefore characterizes relative area use by animals represented in the available telemetry sample and does not indicate the abundance or density of the entire Ural population. Variation in the number of annual routes must also be considered when comparing RRUI values among years.

This study aimed to develop and test an approach to transform open annual GPS routes of the Ural saiga population into a comparable measure of relative space use and to examine its association with vegetation condition. RRUI converts individual annual GPS routes into a normalized district-year indicator. We used it to construct a spatio-temporal panel combining GPS telemetry, MODIS NDVI, climatic indicators, and livestock numbers. The RRUI-NDVI association was estimated using two-way fixed-effects (TWFE) models with sequential inclusion of climatic indicators and livestock numbers. The methodological contribution is a reproducible approach for aggregating available annual GPS routes and integrating them with environmental and other indicators having the same spatio-temporal structure.

NDVI was specified as the response variable because vegetation condition was treated as a potential response associated with relative saiga area use rather than the reverse. RRUI represents the distribution of annual routes based on their observed geography, whereas seasonal NDVI values are generated independently of whether a route crosses a district. The April-October climate window was broader than the May-September NDVI window to capture weather conditions preceding active vegetation growth and continuing after it, as contextual

conditions for the year rather than variables synchronized only with vegetation growth. The testable expectation was therefore a conditional covariance between RRUI and seasonal vegetation condition after controlling for climate and anthropogenic grazing pressure, not a causal effect of saiga on vegetation.

MATERIALS AND METHODS

Study area

The study was carried out in five administrative districts of West Kazakhstan Region of the Republic of Kazakhstan: Akzhaik, Bokey Orda, Zhanakala, Zhanybek, and Kaztal. The choice of districts was determined by the spatial coverage of the available GPS telemetry data for the Ural saiga population: analysis of the annual routes presented in the Atlas of Ungulate Migration (GIUM) (Salemgareyev & Zuther, 2024) showed that their intersection with the territory of West Kazakhstan Region falls predominantly within these five districts. The study region covers approximately 4.1 million ha. The districts were used as second-level administrative spatial units of analysis (ADM2). Their location and the spatial distribution of the 113 annual GPS routes of the Ural saiga population for 2012–2024 are shown in **Figure 1**.

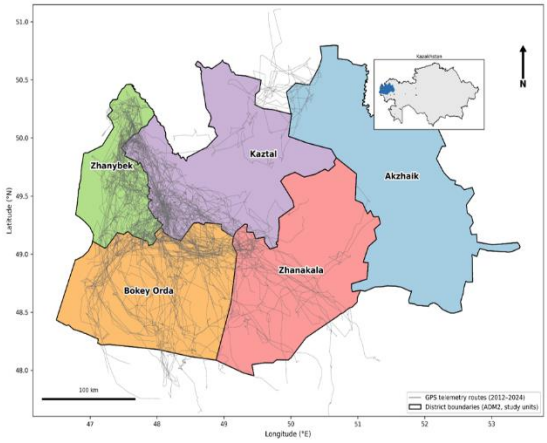


Figure 1. Study area and spatial distribution of annual GPS routes of the Ural saiga population, 2012-2024.

The five study districts are shown as administrative units of the second level (ADM2), and grey lines represent 113 unique animal–year routes. The inset shows the study area's location within Kazakhstan. Administrative boundaries: UNHCR ADM2, 2023. Map display: WGS 84 (EPSG:4326); spatial calculations: WGS 84 / UTM zone 38N (EPSG:32638).

Colors denote the five second-level administrative districts (ADM2) used as spatial units of analysis; grey lines show the 113 unique animal–year GPS routes for the study period. The inset shows the study area within the Republic of Kazakhstan.

West Kazakhstan Region lies within the temperate dry-steppe and semi-desert zone and has a sharply continental climate characterized by cold winters and hot, dry summers. Mean monthly temperatures vary substantially across seasons, while precipitation is generally low: in the analytical panel for 2012–2024, April–October precipitation ranged from 87.806 to 221.554 mm and mean air temperature ranged from 17.901 to 21.178 °C (Jumabayev *et al*., 2026). The main growing season is short, extending from May to September, when spring soil moisture supports vegetation growth, and subsequent summer drying limits its further development. Rangeland vegetation is represented by arid and semi-desert communities that provide forage for both saiga and livestock; consequently, the spatial distribution of vegetation productivity is an important factor for both wildlife and grazing management.

Data sources and preparation

To quantify space use by the Ural saiga population, we used GPS telemetry data, satellite remote-sensing data, climatic data, livestock statistics, and digital administrative boundaries.

GPS telemetry

The main source of data on saiga movements was the published Atlas of Ungulate Migration (Global Initiative on Ungulate Migration, GIUM) (Salemgareyev & Zuther, 2024) — the Kazakhstan_Saiga_Ural_Routes vector layer, covering the period 2012-2024. The original layer contains 184 linear spatial route records; an individual animal's annual route could be represented by several segments. During pre-processing, records belonging to the same animal in the same year were spatially merged using the IndYear identifier. This produced 113 unique animal-year routes for 56 tracked animals. The number of such routes (Nt) ranged from 3 to 23 per year **(Table 1)**.

Table 1. Number of unique annual GPS routes of the Ural saiga population by year, 2012-2024.

Year	Number of unique GPS routes (Nt)	Share of total routes (%)
2012	5	4.4
2013	7	6.2
2014	5	4.4
2015	3	2.7
2016	5	4.4
2017	23	20.4
2018	15	13.3
2019	9	8.0
2020	3	2.7
2021	4	3.5
2022	3	2.7
2023	17	15.0
2024	14	12.4
Total	113	100.0

Remote-sensing data (NDVI). For the assessment of vegetation cover, the MODIS MOD13Q1 Version 6.1 product was used, with a spatial resolution of 250 m and a 16-day temporal step. For each district–year combination, the mean NDVI was calculated for the May–September period of the corresponding year. The MODIS/061/MOD13Q1 collection was used; NDVI raster values were rescaled to the [-1, 1] range by multiplying by the scale factor ×0.0001. Spatial aggregation was performed using the reduceRegions function with the mean reducer and a scale = 250 m parameter, separately for each district polygon. The pixel-level QA mask of the MOD13Q1 product (SummaryQA/DetailedQA band) was not applied during aggregation; all pixels of the 16-day composite were used without additional quality filtering. This limitation is discussed in the Discussion section. The spatial distribution of mean

growing-season NDVI and saiga GPS routes for the selected years is shown in **Figure 2**.

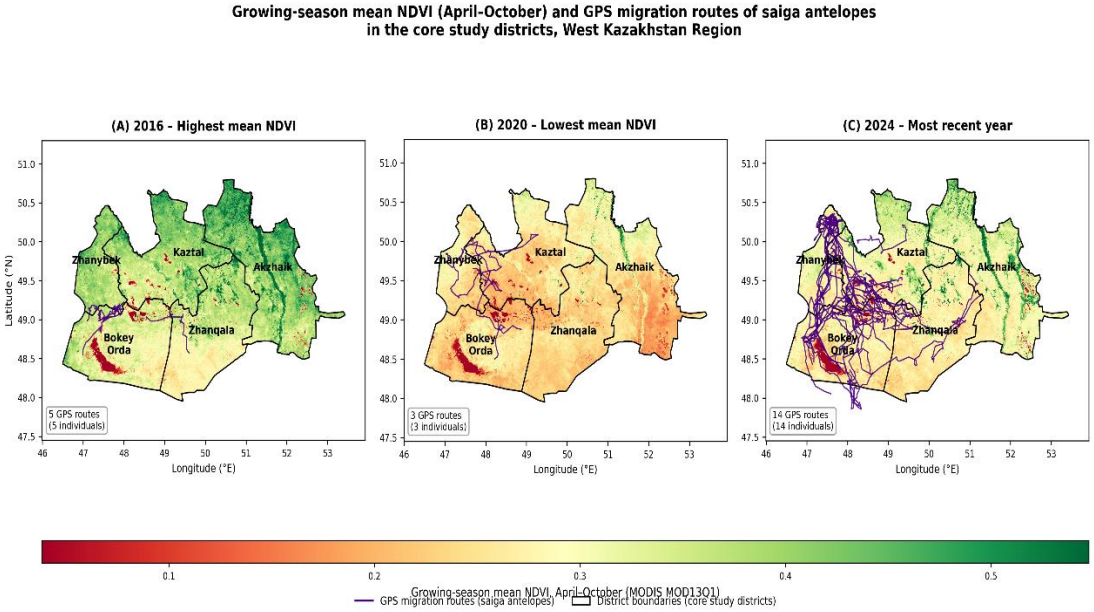


Figure 2. Spatial distribution of mean growing-season NDVI (May–September; MODIS MOD13Q1) and annual GPS routes of the Ural saiga population.

For 2016 (highest mean NDVI), 2020 (lowest mean NDVI), and 2024 (most recent year of observation). The corresponding annual GPS routes are shown after merging the original segments at the animal-year level (Nt = 5, 3, and 14, respectively).

Climatic data

To account for inter-annual and inter-district climatic variability, we used CHIRPS Daily precipitation data (spatial resolution approximately 5.5 km) and ERA5-Land Monthly surface air temperature data (approximately 11 km). Climatic indicators were computed for the April–October period of each year. The corresponding GAUL district geometries were used for their spatial aggregation, after which the resulting values were matched to the analytical panel by district and year.

Livestock data

As an additional indicator of anthropogenic grazing pressure, we used official district-level statistics on the numbers of cattle, sheep and goats, and horses (Bureau of National Statistics 2026). To ensure comparability across species, the original headcounts were converted to livestock units using the formula

$$LU_{jt} = Cattle_{jt} + 0.8\,Horses_{jt} + 0.1\,SheepGoats_{jt}, \quad (1)$$

Where the original headcount figures are expressed in thousand head, and the resulting variable LU_{jt} is expressed in thousand livestock units (LU).

The coefficients for cattle (1.0) and horses (0.8) are based on Eurostat's Livestock Unit (LSU) system (Eurostat n.d.). For sheep and goats, this study uses an author-defined operational coefficient of 0.1. The resulting indicator should therefore be regarded as a standardized measure of relative potential grazing pressure rather than an official Eurostat LSU figure. Administrative boundaries. UNHCR 2023 second-level administrative boundaries (ADM2) were used to delineate the five study districts and intersect them with GPS routes. NDVI was aggregated using a private Google Earth Engine asset (5RAIONOV) containing polygons for Akzhaik, Bokey Orda, Kaztal, Zhanakala, and Zhanybek districts. Names and geometry versions in the metadata were checked and retained. Climate data were aggregated using the corresponding GAUL geometries. Climatic indicators and the main RRUI/NDVI indicators were matched by district name and year. Exact geometric correspondence among UNHCR ADM2 2023, the 5RAIONOV asset, and FAO GAUL 2015 could not be fully verified and is treated as a study limitation.

Spatial preparation of GPS data

The original GPS routes were in WGS 84 / UTM Zone 38N (EPSG:32638; the layer CRS was verified during processing), whereas the administrative boundaries were transformed from EPSG:3857 to the route CRS. After merging GPS segments at the animal–year level, each route was intersected with the five district boundaries. The length of each route segment within each district was then calculated.

The overall sequence of data preparation, RRUI calculation, panel construction, and statistical analysis is shown in **Figure 3**.

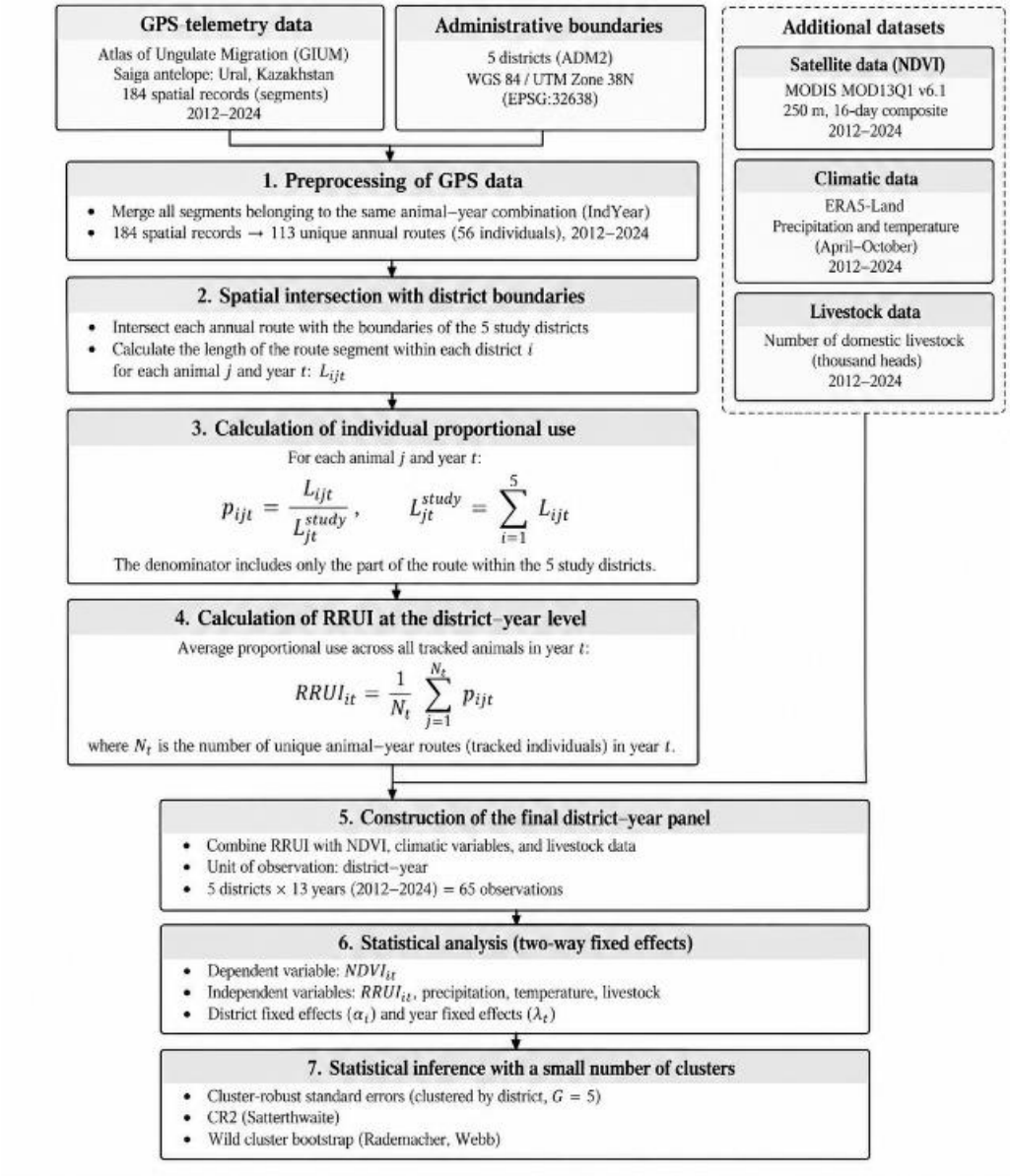


Figure 3. Workflow for data preparation, RRUI calculation, and statistical analysis.

Construction of the Relative Route Utilization Index (RRUI)

The Relative Route Utilization Index (RRUI) was developed to quantify relative space use at the administrative district level. The index is defined as the mean, across tracked animals, of the share of each animal's annual route falling within the corresponding district. The choice of a route-based (linear) data representation is dictated by the source material. Atlas of Ungulate Migration (GIUM) data are provided as aggregated annual animal trajectories rather than as sequences of individual, time-stamped GPS fixes. This limits the applicability of methods based directly on the original point locations, and the absence of time-stamps also precludes models that account for the temporal structure of movement, such as BBMM, AKDE, and CTMM. At the same time, the share of route length within each study district can be calculated directly from the available annual route geometry. The linear approach matches both the research question and the structure of the available data, but it is not the only way to handle linear trajectories; where time-stamped original GPS fixes are available, applying AKDE, CTMM, or similar methods could be a feasible and informative complement to RRUI.

For an animal, the total length of the annual route within the five study districts is defined as:

$$L_{it}^{study} = \sum_{j=1}^{5} L_{ijt}, \quad (2)$$

Where L_{ijt} is the length of the portion of the annual route of an animal falling within district in year. Route segments lying outside the five study districts are not included in the denominator. The individual share of the route falling within district is calculated as:

$$p_{ijt} = \frac{L_{ijt}}{L_{it}^{study}}. \quad (3)$$

RRUI for district in year is defined as:

$$RRUI_{jt} = \frac{1}{N_t}\sum_{i=1}^{N_t} p_{ijt}, \quad (4)$$

Where N_t is the number of unique animal–year routes in year.

Under this aggregation, each annual route receives equal weight regardless of its total length. Because the individual shares are normalized relative to the total route length within the five study districts,

$$\sum_{j=1}^{5} R\,RUI_{jt} = 1. \quad (5)$$

A higher RRUI value means that, on average, a larger share of tracked animals' annual routes is concentrated in the corresponding district. RRUI is not a measure of absolute saiga abundance or density; rather, it characterizes space use by the telemetry sample, not by the entire population. Index values depend on the number and composition of tracked animals in a given year, so account for this when comparing values across years.

RRUI is not a replacement for KDE, BBMM, AKDE, CTMM, RSF, or SSF. These methods address different problems in spatial ecology. In contrast, RRUI is designed to aggregate individual annual GPS routes at the level of defined territorial units and to integrate them with ecological and other data of the same spatio-temporal structure.

Construction of the spatiotemporal panel dataset

After RRUI was calculated, a balanced spatio-temporal panel was constructed in which the unit of observation is the district-year combination. The panel covers five administrative districts over 13 years, from 2012 to 2024, and contains 65 district–year observations (5 × 13). For each observation, the panel includes RRUI, mean NDVI for May-September, precipitation and temperature for April-October, and livestock numbers in thousand livestock units **(Table 2)**.

Table 2. Variables included in the spatiotemporal panel dataset.

Variable	Notation	Unit	Description
Relative Route Utilization Index	RRUI	share (0–1)	Mean share of tracked animals' annual routes falling within the corresponding district
Normalized Difference Vegetation Index	NDVI	dimensionless	Mean NDVI for May–September, calculated from MODIS MOD13Q1 Version 6.1 data
Precipitation	Precipitation	mm	Total precipitation for April–October for the corresponding district and year
Air temperature	Temperature	°C	Mean air temperature for April–October for the corresponding district and year
Livestock numbers	Livestock	thousand LU	Livestock numbers in the corresponding district and year
Number of annual GPS routes	Nt	number of routes	Number of unique animal–year routes available in the corresponding year; used to characterize telemetry sample size

The number of unique annual routes N_t characterizes the telemetry sample size for the corresponding year, but is not included in the TWFE models as a separate explanatory variable. Within each year, N_t is identical across all five districts and is therefore fully absorbed by the year fixed effects. Before the statistical analysis, data completeness, the uniqueness of district–year combinations, and the correctness of source merging were checked; there are no missing values in the final panel.

Statistical model and inference

To assess the conditional statistical association between relative space use by the Ural saiga population and vegetation cover condition, a two-way fixed-effects model (TWFE) was used. District fixed effects account for time-invariant differences between districts, while year fixed effects control for changes over time that are common to all study districts.

The analysis was performed sequentially using three nested specifications. The baseline specification includes RRUI and the district and year fixed effects. The second specification additionally includes precipitation and temperature for April–October. The final specification further includes livestock numbers. The full specification is as follows:

$$NDVI_{jt} = \beta RRUI_{jt} + \gamma_1 Precip_{jt} + \gamma_2 Temp_{jt} + \delta Livestock_{jt} + \mu_j + \lambda_t + \varepsilon_{jt}, \quad (6)$$

Where $NDVI_{jt}$ is the mean NDVI for May–September in district in year; $Precip_{jt}$ and $Temp_{jt}$ are precipitation and temperature for April–October, respectively; $Livestock_{jt}$ is livestock abundance in thousands of LU; μ_j are the district fixed effects; λ_t are the year fixed effects; ε_{jt} is the error term.

The main parameter of interest is the coefficient, which characterizes the conditional statistical association between RRUI and NDVI after accounting for the fixed effects and, in the extended specifications, the included covariates. The coefficient is not interpreted as the causal effect of saiga space use on vegetation cover condition.

For the RRUI coefficient, the null hypothesis:

$$H_0: \beta = 0$$

Is tested against the two-sided alternative:

$$H_1: \beta \neq 0.$$

Models were estimated in R 4.6.1 using fixest 0.14.2 for TWFE estimation and conventional district-clustered standard errors, and clubSandwich 0.7.0 for CR2 with the Satterthwaite correction. Exact wild cluster bootstrap inference was implemented by enumerating all weight combinations in custom R code. Standard errors were clustered by district. Spatial coordinates were transformed using sf 1.1-2, and the reproducible software environment was recorded with renv 1.2.4. The complete code, package versions, and reproducibility files are available in the public repository at https://doi.org/10.5281/zenodo.22884083. Because only five spatial clusters were available, conventional clustered inference was supplemented with CR2 and wild cluster bootstrap using Rademacher and Webb weights.

The complete set of scripts ensuring reproducibility of the analytical panel construction, model estimation, robust standard error calculation, and diagnostic procedures is available in an open repository (Jumabayev, 2026).

RESULTS AND DISCUSSION

Descriptive statistics

The main descriptive statistics of the panel variables are presented in **Table 3**.

Table 3. Descriptive statistics for the spatiotemporal panel variables.

Variable	N	Mean	SD	Min	Max
RRUI	65	0.200	0.187	0.000	0.626
NDVI	65	0.295	0.045	0.218	0.425
Precipitation, mm	65	146.874	31.986	87.806	221.554
Temperature, °C	65	19.015	0.716	17.901	21.178
Livestock, thousand LU	65	104.149	40.055	32.554	214.380

Note. Statistics were calculated for the balanced panel of 65 district-year observations (5 administrative districts × 13 years, 2012-2024).

The mean RRUI value is 0.200, which follows directly from the way the index is normalized: in each year, the RRUI values for the five study districts sum to one. RRUI values range from 0 to 0.626, with a standard deviation of 0.187, indicating pronounced variability in the distribution of observed annual routes across districts and years.

Figure 4 shows RRUI dynamics across the five study districts from 2012 to 2024. The index displays pronounced spatial and interannual variation. The relative distribution of annual routes among districts changed considerably over time, and no district dominated throughout the entire study period. Zero values indicate that none of the annual routes in the available telemetry sample crossed a district in that year; they do not demonstrate the absence of saiga in the district.

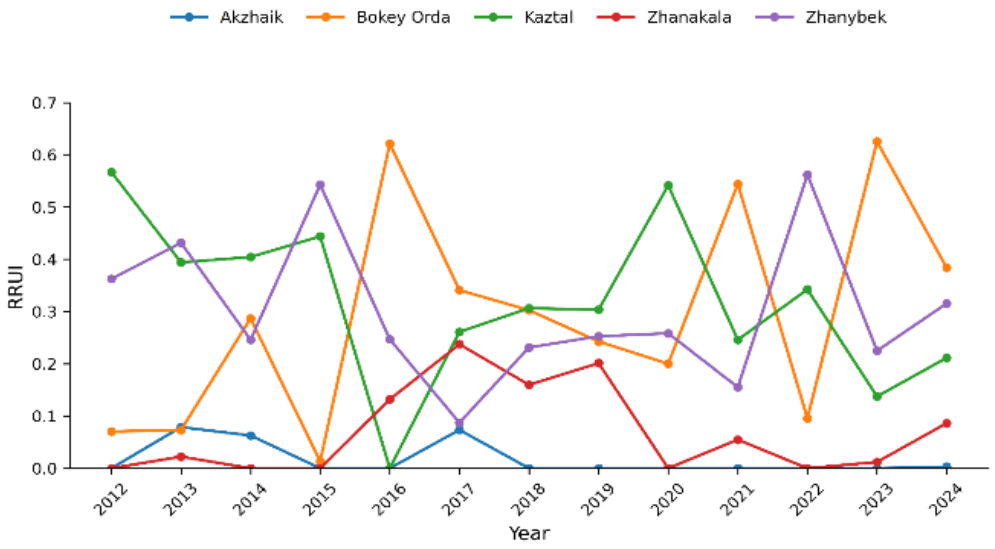


Figure 4. Dynamics of the Relative Route Utilization Index (RRUI) across the five study districts, 2012–2024.
Note. RRUI is the mean share of the annual GPS-route length of tracked Ural saiga individuals occurring within the corresponding district. The annual RRUI values across the five study districts sum to one.

Mean May-September NDVI was 0.295 (SD = 0.045; range = 0.218–0.425). Precipitation ranged from 87.806 to 221.554 mm, with a mean of 146.874 mm. Mean temperature was 19.015 °C, ranging from 17.901 to 21.178 °C. Livestock numbers averaged 104.149 thousand LU and ranged from 32.554 to 214.380 thousand LU.

Relationships among the explanatory variables, including after accounting for district and year fixed effects, are examined below.

Correlation analysis

Before estimating the TWFE models, a correlation analysis of the explanatory variables was performed to provide a preliminary assessment of the linear relationships among them and to detect possible signs of multicollinearity. Results for the raw values are presented in **Table 4**.

Table 4. Pairwise correlation matrix for the explanatory variables.

Variable	RRUI	Precipitation	Temperature	Livestock
RRUI	1	–	–	–
Precipitation	0.366	1	–	–
Temperature	−0.141	−0.285	1	–
Livestock	−0.244	−0.157	0.003	1

Note. Pearson correlation coefficients are shown for 65 district–year observations. The upper triangle of the matrix is omitted owing to symmetry.

The absolute values of the coefficients do not exceed 0.366. The strongest pairwise correlation of RRUI is with precipitation (r = 0.366), while the correlations of RRUI with temperature and livestock are - 0.141 and - 0.244, respectively.

Because the TWFE model accounts for district and year fixed effects, correlations were additionally calculated after removing the corresponding district and year components of the variables **(Table 5)**.

Table 5. Correlations among explanatory variables after accounting for district and year fixed effects.

Variable	RRUI	Precipitation	Temperature	Livestock
RRUI	1.000	–	–	–
Precipitation	−0.009	1.000	–	–
Temperature	0.029	−0.436	1.000	–
Livestock	−0.257	0.133	−0.080	1.000

Note. Correlations were calculated after removing the district and year components of the variables.

After accounting for the fixed effects, the correlations of RRUI with precipitation and temperature are close to zero, while the correlation with livestock is −0.240. The largest absolute correlation among the explanatory variables is between precipitation and temperature (r = −0.436). These values do not indicate a strong linear relationship among the regressors. The correlation matrix reveals no pronounced pairwise linear relationships among the explanatory variables of the final TWFE model.

Baseline TWFE model

Three TWFE specifications were estimated sequentially to assess the conditional association between RRUI and NDVI. The baseline model (M1) includes RRUI and district and year fixed effects. Model M2 additionally includes April-October precipitation and temperature, and model M3 further includes livestock numbers as an indicator of grazing pressure. The results are summarized in **Table 6**.

Table 6. Results of the three TWFE model specifications.

Variable/indicator	M1	M2	M3
RRUI	−0.0184	−0.0163	−0.0172
Cluster-robust SE	0.0111	0.0089	0.0105
p-value	0.173	0.142	0.176
Precipitation	—	0.00062	0.00062
Temperature	—	−0.0557	−0.0558
Livestock	—	—	−0.00007
N	65	65	65
District fixed effects	Yes	Yes	Yes
Year fixed effects	Yes	Yes	Yes
Adjusted R^2	0.814	0.903	0.901
Within R^2	0.022	0.511	0.512

Note. M1 is the baseline model; M2 adds precipitation and temperature; M3 adds livestock numbers. Standard errors are clustered by district.

The RRUI coefficient remains negative and changes only slightly across the three specifications, from −0.0184 in the baseline model to −0.0163 after adding climatic variables and −0.0172 after adding livestock. Under conventional cluster-robust inference, RRUI is not statistically different from zero in any specification.

Adding climatic variables increased within R^2 from 0.022 to 0.511, whereas adding livestock had almost no effect (0.512). In M2 and M3, the temperature coefficients were negative and the precipitation coefficients positive. Temperature was statistically significant at the 5% level under conventional cluster-robust inference (P = 0.005), CR2 (P = 0.017), and WCB with Webb weights (P = 0.033). With only five clusters, the minimum attainable p-value under WCB with Rademacher weights is 0.0625. Neither precipitation nor livestock was statistically significant. Because the conclusions are based on only five spatial clusters, RRUI robustness was assessed using CR2 and wild cluster bootstrap **(Table 7)**.

Table 7. Small-cluster-adjusted inference for the RRUI coefficient.

Model	RRUI	Cluster p	CR2 SE	CR2 p	WCB Rademacher p	WCB Webb p
M1	−0.0184	0.173	0.0113	0.226	0.250	0.212
M2	−0.0163	0.142	0.0106	0.248	0.125	0.109
M3	−0.0172	0.176	0.0124	0.279	0.125	0.131

Note. Cluster p is the p-value based on conventional cluster-robust standard errors; CR2 applies the small-sample correction with the Satterthwaite degrees-of-freedom approximation; WCB is the wild cluster bootstrap. With five clusters, WCB p-values using Rademacher weights are discrete, so results using Webb weights are also reported. Exact WCB p-values were obtained by enumerating all possible weight combinations (32 and 7,776 combinations, respectively).

After applying inference methods that account for the small number of clusters, the RRUI coefficient remained statistically indistinguishable from zero in all three specifications. CR2 produced p-values of 0.226, 0.248, and 0.279 for M1–M3, respectively, while WCB with Webb weights produced p-values of 0.212, 0.109, and 0.131. Thus, the negative direction of the RRUI estimate persists after adding climatic variables and livestock, but the available data do not provide robust statistical support for an RRUI–NDVI association.

Accordingly, the results do not establish a statistically robust relationship between RRUI and NDVI. The relatively stable negative RRUI estimate across all three specifications should be interpreted as a conditional statistical association rather than evidence of a causal effect of saiga space use on vegetation condition.

The principal finding is that the estimated RRUI–NDVI association remained negative across specifications. Still, its statistical robustness was not supported by inference methods accounting for the small number of spatial clusters. The negative RRUI coefficient therefore cannot be interpreted as evidence

that saiga affect vegetation. The observational design supports only a conditional statistical association between the relative distribution of tracked animals' annual routes and NDVI after controlling for district and year fixed effects and the included covariates.

The lack of a statistically robust association is biologically plausible given saiga's high mobility and the multifactorial nature of space use. Migratory ungulate movements depend on vegetation, climate, water, seasonality, landscape structure, anthropogenic disturbance, and habitat connectivity (Johnson *et al*., 2002; Mueller *et al*., 2011; Owen-Smith *et al*., 2020; Kauffman *et al*., 2021a). Saiga movements also vary substantially among years (Singh *et al*., 2010a, 2010b; Singh & Milner-Gulland, 2011; Bunnefeld *et al*., 2011; Koshkina *et al*., 2026). Greater route representation within a district therefore need not coincide with a systematic NDVI change: a district may function as a feeding area, seasonal movement area, or transit corridor, distinctions that seasonal NDVI cannot fully capture.

The findings are consistent with studies of ungulate space use under resource constraints. Bhasin *et al*. (2024) showed that wild ungulates and livestock can coexist through spatial and temporal resource partitioning. Similar patterns occur in semi-arid systems where resource availability, remotely sensed rangeland condition, and land-use fragmentation shape space use (Said *et al*., 2016; Rumiano *et al*., 2020; Tomaszewski *et al*., 2022). Adding district livestock numbers barely changed the RRUI–NDVI estimate. This does not imply that saiga and livestock do not interact; annual district data do not capture spatial overlap, seasonal grazing intensity, or local animal concentrations. Instead, the result highlights the limitations of an aggregated livestock indicator.

The climatic variables markedly increased the models' ability to explain within-panel NDVI variation, while the RRUI estimate changed comparatively little. This is consistent with the important role of climate in vegetation dynamics across arid and semi-arid Kazakhstan and Central Asia (Kolluru *et al*., 2022; Zhuo *et al*., 2025). Route distribution should therefore be interpreted in the context of climate-driven vegetation dynamics without attributing causality to the observed association.

NDVI is an integrative indicator of vegetation condition, not a direct measure of forage biomass available to saiga. District means do not capture differences among vegetation types, phenological stages, or local grazing sites. Reverse directionality is also possible: animals may select areas with particular vegetation conditions, while observed NDVI is simultaneously shaped by precipitation, temperature, and antecedent conditions. Future studies should combine finer seasonal GPS data with indicators of phenology, water, snow cover, infrastructure, and local rangeland productivity and assess relationships across multiple spatial scales.

Anthropogenic fragmentation is also important. Transport infrastructure can alter habitat connectivity and saiga migration patterns (Bizhanova *et al*., 2025), while roads, fences, and industrial development constrain movement or weaken vegetation tracking in other ungulates (Passoni *et al*., 2021; Aikens *et al*., 2022; Jones *et al*., 2022). These mechanisms are not represented directly in the model. If routes are redistributed by infrastructure barriers, RRUI may change independently of NDVI. The result is therefore consistent with a multifactorial understanding of spatial behavior (Kauffman *et al*., 2021a; Abraham *et al*., 2022), but differs from studies showing stronger vegetation relationships with movement or habitat selection (Singh *et al*., 2010b; Aikens *et al*., 2020). This difference may reflect scale: district–year aggregation smooths local and seasonal relationships detectable in original GPS fixes.

RRUI characterizes the relative distribution of aggregated annual routes among administrative districts. It does not measure saiga abundance or density, grazing intensity, or residence time. A high value indicates greater representation of a district in the observed routes, not the proportion of the entire population that used the area. A zero indicates no intersection with routes in the available sample, not the absence of saiga.

The principal statistical limitation is the presence of only five spatial clusters. Although the balanced panel contains 65 district–year observations, conventional cluster-robust inference may not accurately represent uncertainty with so few clusters. Differences among conventional cluster-robust inference, CR2, and wild cluster bootstrap demonstrate sensitivity to the inference method (MacKinnon & Webb, 2017). Persistence of the negative sign alone therefore does not establish a statistically supported association.

The telemetry sample is also heterogeneous: the number of animal–year routes ranged from 3 to 23, and the composition of tracked animals varied among years. Because routes receive equal weight, RRUI in years with small Nt is particularly sensitive to individual movement and describes the sample rather than the entire Ural population. GIUM data comprise annual routes without sequences of GPS fixes or time-stamps. Consequently, transit cannot be distinguished from prolonged area use, seasonal patterns cannot be reconstructed, and fix frequency, temporal autocorrelation, and positioning error cannot be addressed.

District–year aggregation further smooths heterogeneity. The model excludes water availability, snow cover, land use, roads, railways, and fences. Different boundaries were also used: UNHCR ADM2 2023 for RRUI, the private 5RAIONOV Google Earth Engine asset for NDVI, and FAO GAUL 2015 for climate. Exact geometric correspondence was not confirmed, so boundary differences may have affected aggregated indicators. Additional uncertainty arises because pixel-level QA filtering was not applied to MOD13Q1; cloudy or otherwise low-quality pixels were not excluded and may have increased noise, particularly in cloudier years.

Despite these limitations, RRUI is methodologically useful when annual routes are available but high-temporal-resolution GPS fixes are not. It transforms routes into a normalized area–year indicator compatible with ecological and socio-economic data. Because RRUI sums to one across the five districts each year, it captures relative redistribution of observed routes over time. It complements rather than replaces individual-level movement methods.

In practice, RRUI dynamics can identify districts and years in which route distribution changes and can be compared with NDVI, climate, livestock, water, land use, and infrastructure to target more detailed monitoring. The index neither identifies the causes of change nor estimates population size. Its value lies in comparative monitoring, identifying spatio-temporal patterns, and generating testable hypotheses for richer telemetry data, consistent with using ungulate migration maps in conservation decision-making (Kauffman *et al*., 2021b).

CONCLUSION

This study developed the Relative Route Utilization Index (RRUI), a reproducible approach that transforms individual annual GPS routes into normalized district–year indicators and integrates them with remote-sensing data, climatic indicators, livestock numbers, and other spatially aggregated characteristics. Applying RRUI to the Ural saiga population for 2012–2024 produced a balanced spatio-temporal panel of 65 observations across five administrative districts.

The main empirical finding is that the estimated association between RRUI and growing-season NDVI remained negative across all three TWFE specifications but was not statistically robust under inference methods accounting for the small number of spatial clusters. The persistent negative coefficient should therefore not be interpreted as evidence of a biologically confirmed or causal effect of saiga space use on vegetation condition.

The main limitation is that statistical inference is based on only five spatial clusters and a telemetry sample whose size and composition varied among years. RRUI is also calculated from aggregated annual routes rather than original time-stamped GPS fixes. It therefore describes relative space use within the observed telemetry sample, not population abundance or density, habitat residence time, or fine-scale movement patterns.

Despite these limitations, RRUI provides a practical tool for integrating aggregated telemetry data with ecological and conservation indicators at spatial scales relevant to monitoring and management. Changes in RRUI can identify districts and periods with redistribution of recorded routes and help target areas for detailed monitoring. The index should not be used as a direct measure of population size or animal impacts on vegetation.

Further development should validate RRUI using richer telemetry data, finer spatial and seasonal resolution, and comparisons with established movement-analysis methods based on individual GPS fixes. Incorporating additional ecological and anthropogenic factors and applying the approach to other saiga populations and migratory ungulates will help define its scope and limitations more precisely.

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