Telemetry reveals dispersal pathways, excursions, and resting site selection of golden jackals across Alpine–Dinaric and Pannonian landscapes

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Research Article

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Abstract

The golden jackal (*Canis aureus*) has expanded rapidly across Europe, yet quantitative evidence on dispersal routes, exploratory excursions, and resting-site selection across contrasting environments remains limited. We analysed GPS telemetry from twelve jackals tracked in Italy, Slovenia, Croatia, and Serbia from 2018 to 2023. Movement states were segmented using MigrO stay-region clustering and validated with net-squared displacement. We quantified dispersal and excursion duration, distances, trajectories, river and highway crossings, resting-site clusters during non-home-range movements, and pre- and post-dispersal home ranges.

Seven jackals exhibited nine dispersal events, including four short-term dispersals lasting ≤ 2 days and five long-term dispersals lasting 17–61 days. Long-term dispersers frequently crossed major rivers of up to 600 m and highways up to 21 times, indicating high permeability of linear infrastructure. Resting sites used during dispersal were occupied for shorter periods but showed higher fidelity than those used during excursions, consistent with risk-sensitive stopovers. Resting site selection was shaped by interactions with anthropogenic features: agricultural areas were avoided near roads but selected farther away, while proximity to roads was selected outside agricultural areas. Effects of distance to water were context-dependent and reversed in urban areas, while selection decreased with elevation. Post-dispersal home ranges increased in the Alpine–Dinaric region but decreased in the Pannonian region.

Tracked golden jackals dispersed through both natural and human-modified landscapes, with resting site selection reflecting context-dependent trade-offs between cover and human influence. Incorporating wolf presence may further improve future analyses.

1. Introduction

The European populations of the golden jackal (*Canis aureus moreoticus*, Geoffroy 1835) are experiencing the largest documented population expansion in Europe in recent years (Spassov and Acosta-Pankov 2019). The species is spreading from southeastern Europe westward and northward and now appears as a vagrant or with established populations in most European countries (Hatlauf et al. 2021; Sørensen and Lindsø 2021; Rykov et al. 2022; Böcker et al. 2023; de Buruaga et al. 2023; Kojola et al. 2023; Viranta et al. 2025). Its success has been attributed to the absence of larger competitors (Krofel et al. 2017; Newsome et al. 2017), a diverse and often human-facilitated diet (Penezić and Ćirović 2015; Lange et al. 2021), climate change (Cunze and Klimpel 2022), deforestation and road expansion (Spassov and Acosta-Pankov 2019), and the diversity of habitats within its range (Ranc et al. 2025).

The golden jackal is frequently managed as a game species in Europe and has various legal designations (Trouwborst et al. 2015). In its newly colonized range, it establishes new interspecies interactions and ecological roles, which may lead to diverse ecological consequences and potential conflicts with various stakeholders (Lanszki et al. 2006; Ćirović et al. 2016; Krofel et al. 2022; Serva et al. 2023; Kazimirov et al. 2024; Frangini et al. 2025a). Due to its opportunistic nature, conflicts arising from cattle predation (Genov and Vassilev 1991; Yom-Tov et al. 1995; Giannatos 2004) or disease transmission are also becoming more prominent issues (Ćirović et al. 2014; Gherman and Mihalca 2017; Balog et al. 2021; Uzelac et al. 2026). A good understanding of the species' dispersal ability is essential to accurately predict population dynamics and to inform management and conservation decisions (Morales-González et al. 2022). Understanding jackal dispersal could be an important factor in explaining how the population expands and maintains high genetic diversity at the expansion front (Stefanović et al. 2024).

Jackal dispersal has been indirectly reported in some genetic studies (Rutkowski et al. 2015; Stronen et al. 2021; Stefanović et al. 2024) and by records of vagrant individuals found far from known reproductive populations (Möckel 2000; Weingarth et al. 2012; Kowalczyk et al. 2015; Sørensen and Lindsø 2021; Rykov et al. 2022; de Buruaga et al. 2023; Kojola et al. 2023). Telemetry studies have so far documented only a limited number of dispersal events. Lanszki et al. (2017) reported the first telemetry-monitored long-distance dispersal, while Csányi et al. (2025) tracked and reported on a large sample of jackals exhibiting shorter home range shifts.

In this paper, we present a detailed overview of dispersal events in golden jackals from four European countries where dispersal behavior was recorded. We provide the first cross-regional GPS-based synthesis contrasting jackals moving in Alpine–Dinaric and Pannonian regions, and specifically examine variation in dispersal duration, distance, and route, as well as associated behaviors such as pre- and post-dispersal excursions, resting site selection during non-home range movement, and changes in home range size and composition. Additionally, we provide the first cross-regional GPS-based comparison allowing exploratory assessment of differences related to geographic origin and age, the influence of landscape features on movement, and the possible implications of dispersal for gene flow, habitat use, and expansion dynamics. We predicted (i) the use of resting sites during dispersal would be shorter and more spatially constrained than those during excursions, (ii) site selection would reflect a balance between cover and human-modified environments, and (iii) major linear infrastructures would be permeable to dispersers. Finally, we compared pre- and post-dispersal home ranges to assess how range size and composition shifted across contrasting landscapes.

2. Methodology

2.1. Study area and jackal capturing

Data were pooled from four European countries (Italy, Slovenia, Croatia, and Serbia) where telemetry research on jackals is ongoing. Jackals were captured, chemically immobilized, and fitted with GPS collars (details in Table S1 in the Supplementary), and their movements were tracked between

2018 and 2023. Movements were tracked in the regions of Friuli - Venezia Giulia (Italy), Carinthia (Austria), Kranjska (Slovenia), Gorski kotar and Lika (Croatia), and Vojvodina, Šumadija, and Braničevo (Serbia), encompassing multiple habitat types. Jackals in the study area are considered to belong primarily to the Pannonian population with some admixed origins from the Dalmatian population in Italy and Slovenia (Fabri et al. 2014; Stronen et al. 2021; Kovačić et al. 2026). Of all collared jackals, dispersers or those with significant movements outside their home range (HR) were pre-selected based on visual inspection of movement trajectories and later confirmed using a clustering-based approach (2.2. Movement state segmentation).

2.2. Movement state segmentation

Because collar sampling schedules varied among individuals and across time (Table 1), we regularized tracks for clustering by computing daily centroids (arithmetic means of latitude and longitude for each individual per day). Regular tracks with constant sampling (CR1; SR1–SR5) were left unchanged. We segmented tracks using MigrO (Damiani et al. 2015), a QGIS plug-in (QGIS.org 2017; v. 2.6.1, Brighton), which clusters spatial fixes into "stay regions" based on a core radius (ε), a minimum number of neighbors (n), and a presence threshold (δ), using parameters modified from Lanszki et al. (2017).

We set ε to the individual's mean daily step length (median ε produced unrealistically small stay regions for individuals with short-term dispersals), n to the mean number of daily fixes, and δ to 23 (lowered from 30) consecutive days to accommodate one individual (CR1) with a short initial residence period; this did not change clustering outcomes for other individuals.

We then re-applied these clusters to the original fixes using four rules: (i) fixes within a cluster hull were "home range"; (ii) fixes outside but returning to the hull were retained if < 1 day or classified as "excursions" if ≥ 1 day; (iii) fixes between clusters were "dispersal"; (iv) fixes before a cluster were "post-capture". We validated state assignments with Net-Squared Displacement (NSD) profiles, a widely used metric for movement classification and track separation (Edelhoff et al. 2016; Singh et al. 2016; Torretta et al. 2022; Oehler et al. 2025), and inspected apparent discrepancies visually (Supplementary Fig. S1–S12). Two manual corrections are documented in Text box S1 in the Supplementary.

Figure 1. An explanatory graph of the classification correction applied. The left side presents the output of the clustering by MigrO with resampled fixes while the right presents the original points where our criteria were applied. Red dots represent excursions, blue dots are dispersal fixes, green dots are in cluster (home range) fixes and the orange polygon is the MCP hull of the cluster.

2.3. Movement metrics and trajectory analysis

All subsequent analyses were conducted in R (v4.5.0) (R Core Team 2025) using RStudio (v2025.5.0.496) (Posit Team 2025). Movement tracks were created using the "adehabitatLT" package (Calenge 2006; 2025), and descriptive metrics, including duration, distance, and elevation change, were derived for track segments. Dispersal distance was calculated as the distance between HR centroids, except for CR1, where it was calculated from release. Sinuosity was calculated using the "traj" package (McLean and Skowron Volponi 2018), and straightness of dispersals was computed following Benhamou (2004). Highway crossings were identified by intersecting tracks with road layers obtained from OpenStreetMap via the Humanitarian Data Exchange (HDX 2025).

2.4 Resting site analysis

We identified "resting sites" from all non-home-range fixes (dispersal, excursion, post-release) using the "GPSeq-clus" algorithm (Clapp et al. 2021). Parameters were set to a 400 m search radius, a 3-day window, and a minimum number of neighbors equal to the individual's mean daily fixes (5–8) following a sensitivity analysis across 2–5 days and 100–700 m, which showed relatively stable cluster counts across intermediate spatial and temporal settings (Table S2 in Supplementary). To compare excursion and dispersal clusters (hereafter "resting sites"), we applied Student's t-test or Wilcoxon rank-sum test depending on data normality, using metrics including cluster duration, radius, night-fix proportion, maximum foray and fidelity (calculated as the proportion of fixes occurring within the cluster during its active period; distinct from the GPSeq-clus fidelity metric).

Excursion, dispersal, and post-capture resting sites were analyzed together to maximize sample size, ensure representation across individuals, and reduce sampling bias. A Resource Selection Function (RSF) was applied using the "amt" package (Signer et al. 2019). A buffer was delineated around each resting site centroid (derived via "GPSeq-clus"), and 40 simulated fixes were generated per observed point within this buffer. This sampling intensity was chosen because it stabilized the representation of available environmental conditions and produced more stable coefficient estimates across model runs. Buffers intersecting the coastline were trimmed to the coast as sea was not considered available terrain for jackal resting. Candidate RSF models were fitted across buffer sizes ranging from 800 m (~ maximum cluster radius) to 6 km (~ 95th percentile of maximum forays), thereby encompassing biologically plausible availability around resting sites. Buffer size was selected based on the highest area under the ROC curve (AUC) (Table S3 in Supplementary). Environmental covariates were extracted for all fixes. Land cover was derived from CORINE Land Cover 2018 (European Environmental Agency 2019) using the "terra" package (Hijmans 2025) and represented as binary presence/absence. Elevation (meters above sea level (m a.s.l.)) and slope (degrees) were derived from the EU-DEM (Eurostat n.d.) and divided by 100 and 10, respectively, for easier effect size visualization. Waterways, as roads, were obtained from OpenStreetMap via HDX (2025). Distances to the nearest feature (water or road) in each category were calculated in kilometers.

To assess resting site selection, we fitted conditional logistic regression models using the "clogit" function from the "survival" package (Terry et al. 2000; Therneau 2024) in a case-control design stratified by resting site ID. Some land-cover variables exhibited complete separation (absent types within used fixes). To address this and ease interpretation, land-cover types were grouped into ecologically meaningful categories (Table S4,

Supplementary): Urban areas (urban, industrial, human-modified), Forests (broad-leaved, coniferous and mixed woods), Agriculture (cultivated and semi-natural fields and vineyards), Grasslands (open grasslands, pastures, sparse vegetation), Shrubs (transitional woodland shrub and sclerophyllous vegetation) and Water (water courses and bodies). Shrubs were subsequently removed as they inflated VIF values for Forests and Agriculture. The category of Water, represented by only three observed points, was excluded as it lacked ecological relevance; these points were assigned to clusters located adjacent to rivers, reflecting fixes recorded during river crossings to/from those clusters rather than actual resting locations. The influence of wolves was investigated through both presence within wolf range or distance to range edge using data from Kaczensky et al. (2024).

Model term selection was performed using the lowest AIC values with the "stepAIC" function from the "MASS" package (Ripley et al. 2013; Venables and Ripley 2013). Model validation used 5-fold cross-validation, assessing predictive performance using AUC values, calculated with the "pROC" package (Robin et al. 2011). Concordance (C) statistic was derived from the "survival" package. Multicollinearity was low (VIF = 1.01–1.19). The full model included land-cover categories, distances to roads and water, elevation, and relevant interaction terms:

$$\text{logit}(P(\text{use}_{ij} = 1)) = \beta_1\ \text{UrbanAreas}_{ij} + \beta_2\ \text{Agriculture}_{ij} + \beta_3\ \text{Grasslands}_{ij} + \beta_4\ \text{dist\_water}_{ij} + \beta_5\ \text{dist\_roads}_{ij} + \beta_6\ \text{elevation100}_{ij} + \beta_7\ (\text{dist\_waterij} \times \text{UrbanAreas}_{ij}) + \beta_8\ (\text{dist\_water}_{ij} \times \text{Grasslands}_{ij}) + \beta_9\ (\text{dist\_roads}_{ij} \times \text{Agriculture}_{ij})$$

2.5. Home range analysis

Home ranges (HR) were estimated from fixes classified as HR locations, excluding extraterritorial movements (dispersals, excursions, and post-capture movements). For individuals that dispersed, pre- and post-dispersal HR were computed separately. Estimation used the dynamic Brownian Bridge Movement Model (dBBMM) with the "move" package (Kranstauber et al. 2012; 2023) at 50% (core area), 95%, and 99% utilization distributions (UDs). The temporal dependence of dBBMM allowed inclusion of steps with varying fix schedules. Window sizes and margins were set to approximately 3-day and 1-day equivalent fix counts, varying per individual (margin 5–9, window 13–25). Imperfect alignment with fix schedules did not significantly affect HR size or shape, and margin and window size have been noted to have little effect on results in most cases (Smola et al. 2024). Position error was set at 30 m as double the manufacturer-specified error, and steps longer than 13 h (< 0.5% fixes for 6 of the jackals) were excluded to reduce over smoothed bridges (Smola et al. 2024). For three jackals, HRs extending beyond a large river onto the opposite bank were trimmed to the riverbanks to better assess land use (Benhamou and Cornélis 2010). This adjustment was applied conservatively in cases where inclusion of extensive water surfaces would strongly bias land-cover composition. HR composition was calculated as the percentage of each land-cover type from CORINE Land Cover 2018 using the "terra" package, and similarity between starting and ending HRs was assessed with the Bray-Curtis dissimilarity index (Bray and Curtis 1957).

Data visualization was performed using the "ggplot2" package (Wickham 2016) while the maps were made using QGIS ver. 3.40.2.

3. Results

A total of 12 jackals were selected for the study, 8 males and 4 females, yielding a total of 22,707 fixes with a mean success fix rate of 98.08% (Table 1). Jackals from Italy, Slovenia, and Croatia moved mostly within mountainous areas of the Alps and the Dinaric Alps, both inland and near the sea, with some movements in the flatlands of the Venetian-Friulian Plain (Fig. 2a). In Serbia, jackals were recorded mainly around the Danube and Sava rivers, where the flat terrain of the southern Pannonian meets the foothills of the Carpathians (Fig. 2b). Jackals were geographically grouped into the Alpine-Dinaric (Italy, Slovenia, Croatia) and Pannonian (Serbia) groups.

ID	Country	Bio-geographic grouping	Sex	Approximate estimated age (years)	Start of tracking	End of tracking	Fixation schedule	No of days tracked	No of valid fixes	NA percentage (%)
IT1	Italy	Alpine-Dinaric	M	1	09.04.2019.	17.03.2020	4h/6h/10h/11h/13h/19h	344	707	2.62
IT2	Italy	Alpine-Dinaric	F	1	18.11.2021	09.01.2023	4h/6h/10h/14h	418	1275	2.28
SL1	Slovenia	Alpine-Dinaric	F	1.5	20.10.2019	12.10.2020	2h/2.5h/4h/9.5h	359	2137	0.23
SL2	Slovenia	Alpine-Dinaric	M	1.5	21.06.2023	28.02.2024	2h/2.5h/4h/9.5h	253	1478	2.51
SL3	Slovenia	Alpine-Dinaric	F	1.5	18.11.2019	09.08.2020	2h/2.5h/4h/9.5h	266	1615	0.68
SL4	Slovenia	Alpine-Dinaric	M	1.5	19.11.2018	16.05.2020	3h/4h	545	3431	0
CR1	Croatia	Alpine-Dinaric	M	2.5	04.11.2021	25.01.2022	5h	83	373	4.07
SR1	Serbia	Pannonian	M	2	25.04.2022	25.10.2022	3h	184	1423	0.14
SR2	Serbia	Pannonian	M	2.5	06.12.2019	06.11.2020	3h	337	2669	0.52
SR3	Serbia	Pannonian	M	1.5	12.12.2021	18.12.2022	3h	372	2933	0.31
SR4	Serbia	Pannonian	M	2	26.03.2020	16.01.2021	3h	296	2355	0.3
SR5	Serbia	Pannonian	F	1.5	06.11.2021	14.09.2022	3h	313	2311	7.37

Table 1. Summary of GPS-tracked jackals included in the study.

3.1 Dispersal

The separation analysis identified seven of twelve jackals as dispersers, accounting for nine dispersal events. Four dispersals were short-term, lasting 1–2 days, five were long-term (17–61 days), occurring throughout the year (Table S5; Fig. 3; Fig. 4).

The farthest dispersal was by SL4, who traveled from Slovenia through coastal Croatia in a mostly straight line. The route was mainly forested and sparsely populated, ending on a plateau west of the Adriatic coast with forests and grasslands.

CR1 and SL2 had long, relatively straight dispersals, northward, with CR1 the only jackal to descend in elevation (− 572 m) into agricultural and shrubland areas near villages, while SL2 moved from his second HR through his first and crossed the Alps into Austria, traversing elevations up to 1,908 m as well as valleys and settlements.

SR1 and SR4 followed mutually similar routes east from Belgrade toward the Romanian border near the Danube, then returning along different paths. They moved through mostly flat or slightly hilly mosaic landscapes, including suburbs of large cities, both crossing the Sava (~ 300 m) at onset, with SR1 additionally crossing the Danube twice (~ 600 m).

Of the short-term dispersals, IT2 dispersed twice, moving east and ascending in elevation, ultimately settling in the Vipava Valley, a mosaic landscape around a town in Slovenia. Jackal SR1 dispersed by following a meander of the Sava river and around a village to a roughly similar area. Jackal SL2 had one short-term dispersal to the northwest before proceeding to his long-term dispersal through his first HR. None of the short-term dispersal jackals had resting sites during dispersal.

Beside elevation changes, river crossings and highways also posed little impediment to dispersing jackals. Five of the jackals demonstrated frequent highway crossings, up to 21 events (Table S5). All dispersals except those of SR1 and SR4 occurred through areas of wolf distribution (Kaczensky et al. 2024).

3.2 Excursions

A total of 48 excursions were identified among 11 of the 12 jackals, with SR1 having none. The mean duration of excursions was 4 days 23 hours (± 5 days 17 hours) and mean distance of 10.1 ± 6 km (Fig. 5). Two outliers in duration and distance were observed: IT1, whose excursion lasted 32 days and 17 hours and who traveled 24.36 km from his HR, and SL3, who traveled 37.75 km over 6 days. Both excursions could be considered as attempted dispersals due to their extent; however, IT1's movement was not classified as such because no destination HR could be identified before data collection ended, even though later camera trap records confirmed his prolonged presence in the area, while SL3 returned to her original HR. Additionally, highway crossings were recorded: eleven for SL2 and eight crossings during two excursions of SL1.

Regarding long-term dispersers, only SL4 exhibited a 2-day excursion one day before dispersing in the same direction. Jackal SL2 was stationary for more than a month prior to his long-term dispersal, and SR1 and SR4 had no documented excursion preceding their dispersals. For the short-term dispersals, IT2 had none immediately preceding dispersal, and SL2 had one 15-day excursion which after a 3-day stopover continued into a short-term dispersal. Jackal SR2 had no excursions in the 6 months before his dispersal and, in fact, dispersed in the opposite direction from its previous explorations. Although not classified as dispersing, IT1 had six excursions before his longer 32-day excursion. After dispersal, SR4 had only one excursion, while CR1 had 3, SL2 had two, and SL4 had 10. Dispersals and excursions occurred throughout the year, with the lowest frequency during summer (Fig. 4).

3.3 Resting sites

A total of 70 resting sites from nine jackals were analyzed: 38 from excursions, 28 from long-term dispersals, and 4 from post-capture movements. No resting sites were detected for short-term dispersals. Clusters were rarer in the Alpine-Dinaric group (Table S5). Excursion and dispersal resting sites differed in three key metrics: duration, fidelity and maximum foray.

The durations of stay at resting sites differed significantly ($W = 871.5$, $p = 0.002$), with stays at excursion resting sites lasting longer (median 77.7 h, IQR 40.5–100) than stays at dispersal resting sites (median 43.2 h, IQR 24–54.75; Fig. 6a). Fidelity was higher in dispersal resting sites (median 98%, IQR 78–100%) than in excursions (median 66%, IQR 47–84%; $W = 229.5$, $p < 0.001$; Fig. 6b). Maximum forays were larger during excursions (median 1.60 km, IQR 0.77–3.70) than during dispersals (median 0.42 km, IQR 0.25–0.95; $W = 939$, $p < 0.001$; Fig. 6c).

Night-to-day fixation proportions ranged from entirely night to entirely day, with a mean of 50% ± 27%, and did not differ between excursions and long-term dispersals. Resting site radius also showed no significant difference, with an overall mean of 285.4 ± 132.2 m.

The resting sites comprised 903 fixes, which, together with pseudo-absence fixes, resulted in a total of 37,023 fixes used in the resting site selection model. Model performance was optimal at a buffer size of 5 km; however, selection coefficients were broadly consistent in direction and magnitude across all buffer sizes, with only modest performance gains beyond ~ 4 km, indicating a plateau and stable habitat-selection signals between 4 and 6 km (Table S3 in Supplementary). The model showed moderate concordance ($C = 0.71$). Overall discrimination was relatively modest, with an AUC of 0.656 (95% CI: 0.64–0.672). Cross-validated AUC values ranged from 0.637 to 0.686 (mean = 0.654) indicating stable predictive performance.

Forests, wolf range (presence and distance from it) and slope were not significantly selected for or against while agriculture, urban areas, grasslands, distances to water and roads, elevation and/or their interactions had significant influences on resting sites selection (Fig. 7; full model summary in Table S6 in the Supplementary).

Selection for agricultural areas depended strongly on distance to roads. At zero distance to roads, agricultural areas were avoided ($\beta = -1.13$, $OR = 0.32$, $p < 0.001$), but this effect weakened and reversed with increasing distance due to a strong positive interaction with distance to roads ($\beta = 2.79$, $OR = 16.21$, $p < 0.001$). The net effect of agriculture became neutral at approximately 0.41 km from roads and positive beyond this distance. Outside agricultural areas, selection decreased with increasing distance to roads ($\beta = -1.51$, $OR = 0.22$, $p < 0.001$), indicating selection for areas closer to roads.

Distance to water was generally associated with reduced selection with smaller distances ($\beta = 0.26$, $OR = 1.29$, $p < 0.001$), but this relationship varied across habitats. In urban areas, the effect of distance to water was strongly reduced ($\beta = -3.37$, $OR = 0.03$, 95% CI: 0.01–0.14, $p < 0.001$), resulting in an overall negative slope ($\beta = 0.26 - 3.37 = -3.11$), indicating strong selection for areas closer to water. In grasslands, the effect was also reduced ($\beta = -0.55$, $OR = 0.57$, $p = 0.004$), yielding a weaker positive slope ($\beta = 0.26 - 0.55 = -0.30$), indicating a shift toward slight preference for areas closer to water. Selection decreased with increasing elevation ($\beta = -0.12$, $OR = 0.89$ per 100 m a.s.l., $p < 0.001$). No clear main effects were detected for urban areas or grasslands. Marshes and water were almost exclusively avoided (Table S3 in Supplementary).

3.4 Home ranges

A total of 20 HRs (95% UD dBBMM) were estimated from 12 jackals: 12 were first-order, 6 second-order, and 2 third order. HR sizes ranged from 1.6 to 91 km² (median: 11.27 km², IQR: 8.47–21.82 km²) (Table S7 and Figs S14–S19 in the Supplementary). Starting HR were smaller than ending HR for jackals dispersing in the Alpine-Dinaric group, while the opposite pattern was observed in the Pannonian group. Few consistent land-use changes were detected (Tables S8 and S9, Figs S14–S19 in the Supplementary). Use of broad-leaved forests decreased (− 0.42% to − 50.51%, 6/8 dispersers), in favor of other forest types. Complex cultivation patterns increased in five dispersals (+ 2.95% to + 54.9%). The share of human-modified terrain increased for all jackals but rarely exceeded 5% for any category. Among dispersals in the Alpine-Dinaric group, the share increased for more open areas – natural grasslands (+ 0.01% to + 33.1%, 4/5 dispersals) and pastures (+ 0.62% to + 5.26%, 5/5 dispersals). HR dissimilarity ranged from 0.195 (IT1, first dispersal) to 0.847 (SR4), with a mean of 0.588 (Table 2).

Table 2
Comparison of dispersing jackal starting and ending home ranges and associated changes in size and composition after dispersal

ID	Bio-geographic grouping	Starting HR size (km^2)	Ending HR size (km^2)	HR size change (%)	Starting HR duration (days)	Ending HR duration (days)	Bray-Curtis dissimilarity index
IT2 (first dispersal)	Alpine-Dinaric	11.41	41.65	265.06	51	57	0.195
IT2 (second dispersal)	Alpine-Dinaric	41.65	91.14	118.82	57	309	0.486
SL2 (first dispersal)	Alpine-Dinaric	7.49	8.80	17.59	90	34	0.403
SL2 (second dispersal)	Alpine-Dinaric	8.80	26.26	198.33	34	89	0.671
SL4	Alpine-Dinaric	6.47	10.99	69.99	94	435	0.592
CR1	Alpine-Dinaric	/	2.68	/	/	48	/
SR1	Pannonian	22.55	11.14	-50.62	13	114	0.680
SR2	Pannonian	11.09	1.60	-85.58	278	58	0.238
SR4	Pannonian	20.26	13.27	-34.51	32	205	0.847
Mean		17.21	23.08	60.69	81.13	149.89	0.514
Mean Pannonian		17.97	8.67	-56.90	107.67	125.67	0.588
Mean Alpine-Dinaric		15.16	30.25	133.96	65.20	162.00	0.469

4. Discussion

Dispersal in our sample varied in duration, distance, and route. Alpine-Dinaric jackals traveled along relatively straight paths with moderate sinuosity (Table S5), suggesting cautious yet goal-directed movement, which may reflect heightened risk perception during dispersal. The Pannonian group followed more meandering paths, like the more tortuous dispersal patterns reported by Lanszki et al. (2018) in Hungary, possibly due to the relative scarcity of wolves in this area, which allows jackals to roam more freely. However, given the limited number of dispersal events, these interpretations should be viewed as indicative rather than definitive.

Based on our sample, short-term dispersals lasted from several hours to a few days, while long-term dispersals typically extended 20–30 days (excluding return movements of SR1 and SR4), although a shorter long-term dispersal of 12 days has been reported (Lanszki et al. 2018). Most other canids exhibit longer dispersals, including coyotes (Harrison 1992), wolves (Morales-González 2022), and red foxes (Gosselink et al. 2010; Walton et al. 2018). An exception is the African wild dog (mean = 19 days; Woodroffe et al. 2020).

Movement distances for short-term dispersals were comparable but at the lower end of values reported for jackals undergoing range shifts (1.46–56.43 km; mean 14.37 km; Csányi et al. 2025). Long-term dispersals were several-folds longer and consistent with previously reported jackal dispersals (61.2 km; Lanszki et al. 2018). However, multiple instances of vagrant individuals being recorded or shot far from the nearest populations have been reported (Möckel 2000; Weingarth et al 2012; Kowalczyk et al. 2015; Rutkowski et al. 2015; GOJAGE blog 2021; Sørensen and Lindsø 2021; Rykov et al. 2022; de Buruaga et al. 2023; Kojola et al. 2023). Some of these sightings occurred over 1000 km from the nearest population, suggesting an even greater dispersal ability than recorded here. Dispersal distances in coyotes, wolves, red foxes, and African wild dogs vary, with coyotes and wolves generally dispersing similar or greater distances than observed in this study (Gese et al. 1989; Harrison 1992; Kolbe and Squires 2004; Sasmal et al. 2019; Zepeda et al. 2021; Morales-González 2022), whereas red foxes and African wild dogs generally disperse shorter distances (Coman et al. 1991; Gosselink et al. 2010; Walton et al. 2018; Woodroffe et al. 2020).

Throughout dispersal, jackals moved through landscapes ranging from expansive natural forests and agricultural areas to mosaic habitats and densely populated neighborhoods. They demonstrated the ability to overcome various ecological and anthropogenic barriers. Multiple cross-border movements, as well as river and highway crossings, were recorded in several individuals. The high permeability of linear barriers may have important management implications as identifiable hard barriers for jackals become fewer in number. Deep snow, extreme frosts, extensive, high forests or unbroken scrub, heavily intersected (steep) relief, intensively cultivated areas without cover, intensively used urban areas, and the presence of wolves have previously been identified as factors limiting golden jackal occurrence (Spassov 1989, cited in Spassov and Acosta-Pankov 2019; Giannatos 2004). Our results showed that jackals can overcome these barriers, with SL2 dispersing through the Alps in late autumn (November-–December) at elevations of 1000-–1800 m a.s.l., while SL4 and CR5 moved through continuous forested areas across at least seven and two wolf pack territories, respectively. All Alpine-Dinaric jackals dispersed within areas of known wolf distribution (Kaczensky et al. 2024). Jackals living in more natural high mountain forested areas have been observed to occur sympatrically with other large carnivores (Guimaraes et al. 2021), and to be increasing in sympatry with wolves in some areas (Frangini et al. 2025b). In contrast, SR2 and SR4 dispersed only to the edge of wolf distribution in eastern Serbia before returning, suggesting that wolf presence may potentially constrain dispersal when jackals lack prior exposure. These patterns indicate that

jackals can disperse through wolf-occupied landscapes, but lack of experience with wolves may influence dispersal success, however limited sample size limits us from making conclusive statements.

Most tracked jackals were younger than 2 years when significant excursions or dispersals occurred (Tables 1 and 2). Helpers, offspring that remain in the natal group and contribute to raising subsequent litters, are documented in golden jackals (Pecorella et al. 2022; Custers et al. 2024), and several dispersal events (SR1, SR4, and the major excursion of SL2) coincided with the pup-rearing period (~ April–May), when helper departure has been reported (Custers et al. 2024). Other, younger individuals, initiated dispersal earlier in the year (IT2, SL4, and the excursion of IT1) possibly relating to the breeding season, whereas older individuals (SL2, CR1, SR2) dispersed later in the year, although we cannot exclude initial dispersal starting earlier. For example, SL2 was likely already in a transient phase prior to capture, as he was trapped in a high-altitude area outside known jackal presence with no other individuals detected despite intensive monitoring. Capture itself may also have contributed to dispersal in some cases (CR1 or SR1). Timing of dispersals and extensive excursions varied, although they broadly matched reported peaks in range shifts (Csányi et al. 2025). Changes in HR location have been documented in jackals following partner loss (Csányi et al. 2023). As jackals are a hunted species in most of the study area (Trouwborst et al. 2015) and are frequently subject to road mortality (Frangini et al. 2022), recurrent social disruption through mate loss may trigger dispersal in at least some individuals. For other canids, dispersal peak occurs most commonly in January to March in coyotes (Harrison 1992; Gese et al. 1996; Kolbe and Squires 2004; Sasmal et al. 2019), from late autumn through spring in wolves (Morales-González 2022), and from late autumn through early spring in foxes (Gosselink et al. 2010; Walton et al. 2018).

Out of all jackals studied in the study area, dispersal events were recorded in ~ 20% of individuals. Csányi et al. (2025) reported a 37% frequency of range shifts. In our sample, only one of the dispersing individuals was female. In contrast, a previously documented case of long-distance dispersal involved a female (Lanszki et al. 2018), and Csányi et al. (2025) found that range shifts occurred approximately twice as often in females. Genetics based research however suggest that there is no sex bias in dispersal (Stefanović et al. 2024).

Jackals dispersed in nearly all cardinal directions, both along the northwestern trajectory of population expansion (Spassov and Acosta-Pankov 2019) and against it. Notably, one cross-population dispersal occurred: SL4 dispersed from Slovenia to Dalmatia (Croatia), moving from the Pannonian to the Adriatic (Dalmatina) population (Ranc et al. 2025). When genotyped, Slovenian jackals generally align with those from Croatia (proper), Serbia, and other Pannonian jackals; however, some have shown Dalmatian ancestry (Stronen et al. 2021; Kovačić et al. 2026). The genetic profiles of jackals sampled in Italy indicate some Pannonian or admixed origins (Fabbri et al. 2014; Kovačić et al. 2026), while some research suggests genetically distinct subpopulations in Austria and Hungary (Stefanović et al. 2024). The genetic structure of these (sub)populations, together with the dispersals of SL4, IT2, and SL2, indicate cross-border and cross-population mixing, although direction and magnitude remain unclear. Long-distance dispersal has been suggested as a possible mechanism for establishing new populations by Rutkowski et al. (2015), particularly in Eastern Europe (Stefanović et al. 2024), as evidenced in some recent colonizations (Männil and Ranc 2022). Shorter, stepping-stone mechanisms have been proposed for the Pannonian population (Fabbri et al. 2014; Stefanović et al. 2024). The results suggest that both mechanisms occur in our study area. Multidirectional and multimethod dispersals may be key to maintaining high genetic diversity at the expansion front (Stefanović et al. 2024), likely supporting the jackal's success in expansion.

We could not confirm whether some of the dispersals were group attempts. Rutkowski et al. (2015) suggested that long-distance group dispersal may be a possible mode of colonization. This aligns with larger-scale dispersals involving smaller groups moving in several distinct, repeated waves, as proposed by Stefanović et al. (2024). The absence of sex bias, diversity in age, and discrepancies between our findings and other research lends some support to this idea.

Pre-dispersal exploration has been documented in numerous carnivore species, including badgers (Roper et al. 2003), wolverines (Vangen et al. 2001), lynxes (Zimmerman et al. 2005; Samelius et al. 2012), wolves (Gese and Mech 1991; Boyd and Pletscher 1999; Wabakken et al. 2007; Mancinelli and Ciucci 2018), coyotes (Morin and Kelly 2017), and red foxes (Woollard and Harris 1990), as well as in a jackal individual (Lanszki et al. 2018), which showed both pre- (n = 6) and post-dispersal (n = 7) excursions. Exploratory movements may allow juveniles and prospective dispersers to assess conditions beyond their natal range and gather information on surrounding habitat before selecting a dispersal direction (Debeffe et al. 2013). In this study, only two jackals showed clear pre-dispersal excursions (Fig. 4), suggesting similar or less exploratory behavior compared to other carnivores, in which pre-dispersal exploration occurs in 40–75% of dispersing individuals (Woollard and Harris 1990; Gese and Mech 1991; Boyd and Pletscher 1999; Vangen et al. 2001; Zimmerman et al. 2005; Mancinelli and Ciucci 2018). However, some individuals exhibited earlier dispersal or extended area use before their final dispersal (IT2, SL2, SR1, SR4) or similarly long excursions (IT1).

Post-dispersal excursions were more frequent in the Alpine-Dinaric group than in the Pannonian group, where SR4 was the only individual to exhibit a very brief, early post-dispersal excursion. Given the smaller settled areas in the Alpine-Dinaric region (Table S5), jackals in this group may need to forage beyond their HR due to lower habitat quality, or these movements may represent pre-dispersal excursions preceding further dispersal, as multiple dispersal events by the same individuals were observed.

The resting site analysis revealed clear differences between excursion and dispersal resting sites. Jackals at the resting sites during excursion stayed about twice as long but showed lower fidelity, spent less time in them and traveled up to four times farther during forays. This pattern suggests higher perceived risk during dispersal, with excursion sites functioning as temporary bases with intermittent returns, in contrast to brief, tightly managed dispersal stopovers.

When selecting resting sites, jackals showed no clear main effects for most habitat classes, with selection structured by interactions with anthropogenic features and topography. Forests were not significantly selected for or against. In contrast, wolves show strong preferences for natural habitats when selecting resting sites, both within HRs and during dispersal (Llaneza et al. 2016; Bojarska et al. 2021; Torretta et al. 2022; Rio-Maior et al. 2025), and consistently avoid human infrastructure (Theuerkauf et al. 2003; Zimmermann et al. 2014; Llaneza et al. 2016; Bojarska et al. 2021; Rio-Maior et al. 2025). In contrast, jackals in this study did not show a clear overall response to urban areas, but selection was strongly modified by proximity to water. Proximity to water in urban areas may reflect the use of small watercourses as cover and movement corridors. In the Pannonian (Serbia) subset, irrigation channels frequently serve this function (Fenton et al. 2021; Pantelić et al. 2024). The effect of distance to water in grasslands, which showed no main effect, may reflect a similar process of seeking cover, although much less strongly. In other areas distance to water had a positive but relatively weak effect, with approximately 29% greater selection per 1 km increase in distance. Jackals are known for their behavioral plasticity and tolerance of human-modified landscapes, and proximity to human settlements has been suggested to provide a refuge from wolves (Ranc et al. 2026). Thus, resting near settlements may reduce predation risk from wolves for dispersing jackals.

Non-dispersing jackals have been shown to avoid artificial surfaces and agricultural areas (Gaál et al. 2025), in contrast to the more context-dependent selection observed in this study. Selection for agricultural areas depended strongly on distance to roads, shifting from avoidance near roads to positive selection beyond ~ 0.41 km. These distances likely correspond to forest(shrub)-agriculture edges, which provide both cover and enhanced foraging opportunities and are recognized as preferred habitats for jackals (Fenton et al. 2020; Csányi et al. 2025; Gaál et al. 2025). The selection of agricultural areas farther from roads in our study likely did not reflect openness alone, as grasslands showed no comparable pattern. Instead, it may indicate avoidance of the higher levels of human disturbance associated with agricultural areas near roads, while selection for proximity to roads in other habitats may reflect their use as movement corridors or foraging sites, where benefits outweigh disturbance. Nonlinear relationships may warrant further exploration.

Hinton et al. (2015, 2016) examined so-called “biding areas” (50% UD HR during transient movements) in coyotes and red wolves. They analyzed stopover habitat selection during transience. They found that coyotes did not show significant differences between the 50% and 95% UDs of resident and transient individuals, whereas red wolf biding areas contained more coastal bottomland and wetlands and less agriculture than resident core areas (50% UD). Because our resting site clusters combined both excursions and dispersals, and HR samples were small and heterogeneous, we did not compare resting site and HR core compositions. Future studies could test whether jackals, like red wolves, select different resting habitats during non-HR movements than within established HR.

Within local resting site areas, jackals preferentially selected lower elevations, likely corresponding to zones with greater human infrastructure, particularly in alpine regions where settlements are concentrated in valley bottoms. Jackals generally tend to select lower altitudes (Bijl et al. 2025) and inhabit less rugged areas (Frangini et al. 2025b). A similar pattern was observed in dispersing wolves, which might select lower elevation and slope in their resting site selection (Rio-Maior et al. 2025).

Wolf presence was not significant in the model, likely because of the coarseness of the available distribution mapping. Given its suspected importance, further research may focus on investigating this effect.

Jackals showed considerable variation in how much their new HRs differed from previous ones. Geographical differences were apparent, with Alpine-Dinaric jackals generally increasing HR size, while Pannonian jackals tended to decrease it. In related species, a dispersing male wolf in mountainous Bulgaria exhibited a more than twofold increase in HR size (Tsingarska et al. 2024), whereas two dispersing wolves in Czechia showed contrasting patterns, with both substantial decreases (by a factor of 2.5) and increases (by a factor of 3.5) reported (Vorel et al. 2024). In contrast, a previously tracked dispersing female golden jackal showed no change in HR size (Lanszki et al. 2018).

Csányi et al. (2025) found that HR size following range shifts was mainly influenced by range sequence, with third HRs generally being the largest – a pattern also observed in some individuals in our sample (IT2 and SL2). All three Pannonian jackals showed reductions in HR size. For SR1 and SR4, these reductions likely reflect a shift from predominantly intensive agriculture to a more mosaic landscape, including increased complex cultivation, industrial or commercial units, and closer proximity to human settlements (Belgrade suburbs). Proximity to human settlements has been linked to smaller HRs in jackals and other canids (Rotem et al. 2011; Šálek et al. 2015).

Since open habitats increased slightly within the Alpine-Dinaric group, this likely contributed to the observed HR expansion, as shifts into more open, fragmented habitats with reduced cover likely required greater space use, resulting in larger HRs. The largest HR observed was IT2’s second, which likely represents an outlier in this study, exhibiting more nomadic than residential movement. Although not classified as a dispersal, IT1’s final excursion, lasting 32 days, was the only instance of a jackal moving from agricultural areas near a settlement into forested mountains, despite his more nomadic than residential movement.

Taken together, these observations suggest that changes in range size and composition are not a uniform consequence of dispersal, but instead reflect individual strategies, regional landscape characteristics, and habitat composition. Differences between the Alpine-Dinaric and Pannonian jackals, for example, may be shaped by the distribution of land cover types, highlighting the flexibility and context dependence of jackal spatial behavior. Overall, their dispersal patterns do not follow a simple source-sink dynamic related to habitat composition, but more likely reflect complex habitat use and population processes.

5. Conclusion

Golden jackals in Alpine–Dinaric and Pannonian Europe disperse via both natural and human-modified corridors, frequently traversing rivers and major highways. Resting-site behavior during dispersal is characterized by brief, spatially constrained stopovers, consistent with risk-sensitive movement. Resting site selection was shaped by context-dependent interactions, reflecting a balance between cover, anthropogenic disturbance, and resource use. Regional differences in post-dispersal home-range size suggest context-dependent strategies rather than uniform source–sink dynamics. Incorporating predator landscapes into movement and resting-site models will sharpen inference on the mechanisms enabling rapid range expansion.

Declarations

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Statements and Declarations

The authors have no relevant financial or non-financial interests to disclose.

Ethics approval

In Serbia, no specific protocols or licenses were required for non-laboratory work with jackals, so standard protocols for work with protected mammals were applied. These were specified under licenses to conduct fieldwork as part of field teaching and research issued through contracts with the Ministry of Education, Science, and Technological Development (License no: 353-01-06/2022-04). For Slovenia, all capture and handling procedures complied with Slovenian national animal welfare legislation and were approved by the relevant authorities (Ministry of Environment and Spatial Planning; permit no: 35601-115/2017-4 and Ministry of Food, Agriculture and Forestry; permit no: 341 – 159/2024/7). In Italy, the release of recovered jackals from care centers has been communicated to the regional Biodiversity and Hunting Services. Capturing and handling for scientific purposes was authorized by the Autonomous Region of Friuli Venezia Giulia (Regional Government Decree, Prot. No. 0193777/P/GEN, dated 19/10/2022. The permit used in Croatia was from the Ministry of Environment Protection and Energetics: KLASA: UP/I-612-07/19–48/76.

Data availability

The datasets generated and/or analysed during the current study are not publicly available due to ownership restrictions, but may be available from the corresponding author on reasonable request.

Author contributions

Ilija Pantelić performed the analyses and wrote the first draft of the manuscript. Ilija Pantelić, Hubert Potočnik, and Duško Ćirović contributed to the study conception and design. All authors contributed to data collection, fieldwork, resources, and/or interpretation of the results. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Figures

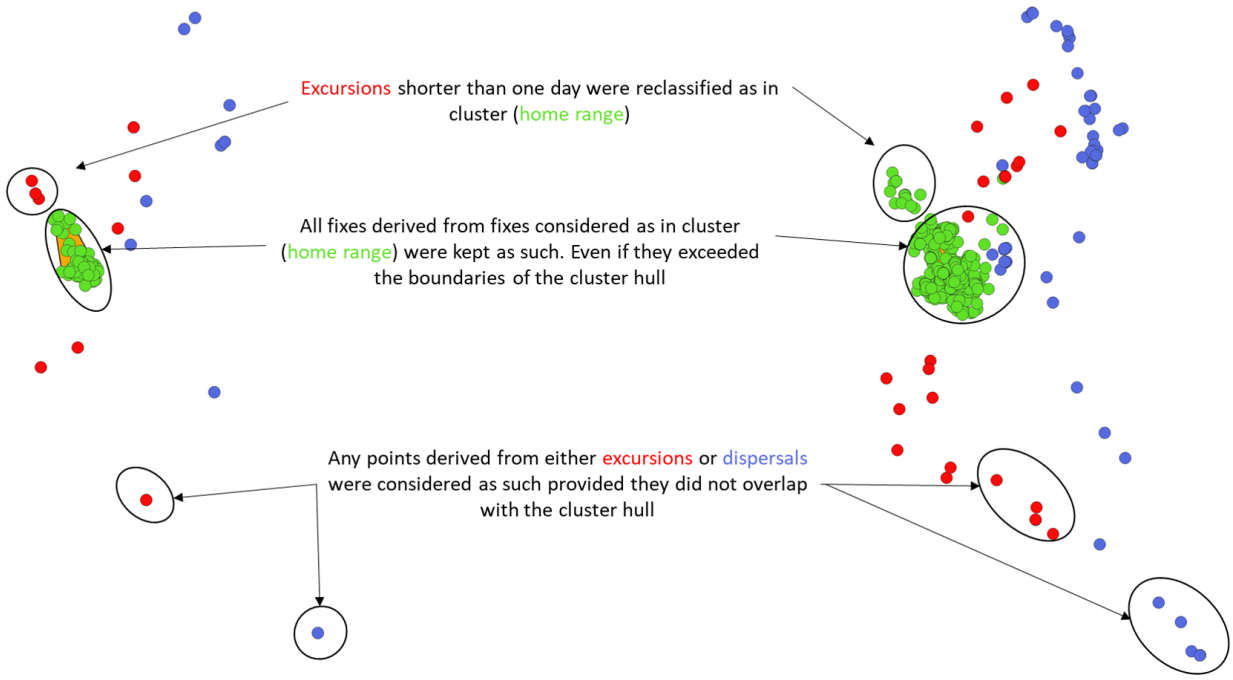

Figure 1

An explanatory graph of the classification correction applied. The left side presents the output of the clustering by MigrO with resampled fixes while the right presents the original points where our criteria were applied. Red dots represent excursions, blue dots are dispersal fixes, green dots are in cluster (home range) fixes and the orange polygon is the MCP hull of the cluster.

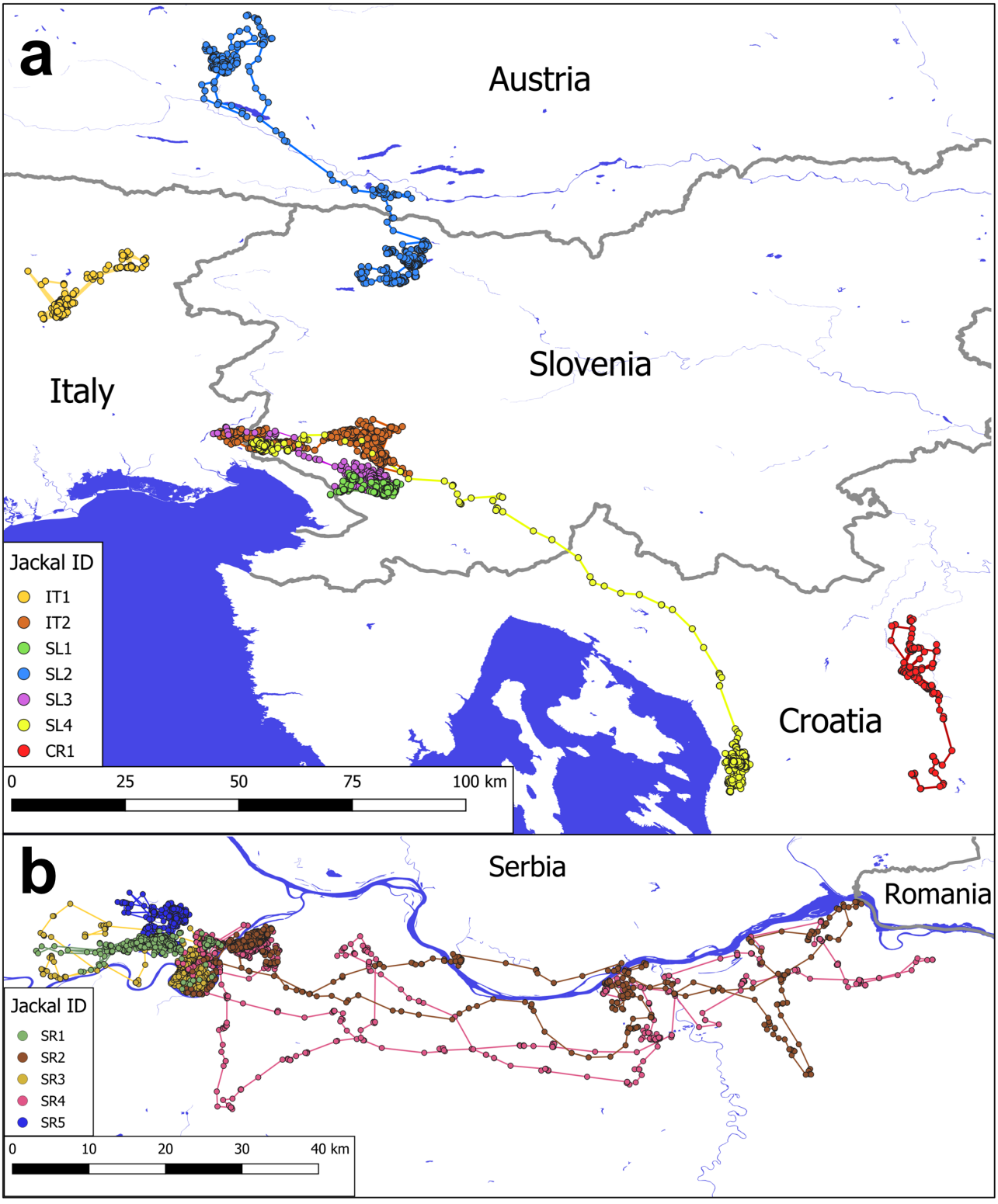

Figure 2

GPS-tracks of collared jackals in Italy, Austria, Slovenia and Croatia (a) and Serbia (b). Different collared dots signify individual jackals

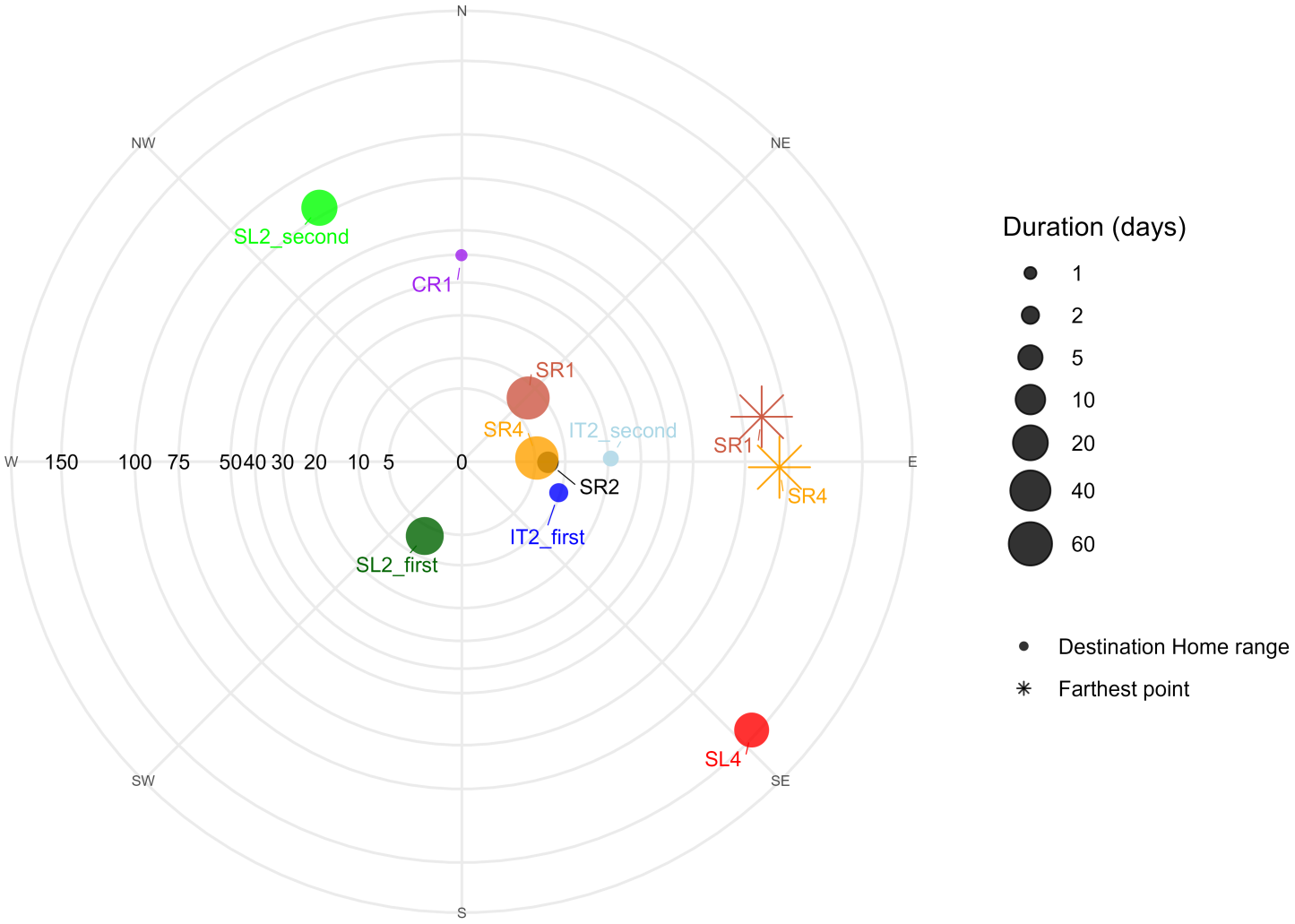

Figure 3

Radar chart of dispersal events. Distance in kilometers and direction of points from center represent dispersal direction and direction to destination HR. Circle sizes indicate duration of dispersal events. Farthest points for SR1 and SR4 are additionally represented by stars to illustrate the extent of the dispersal event.

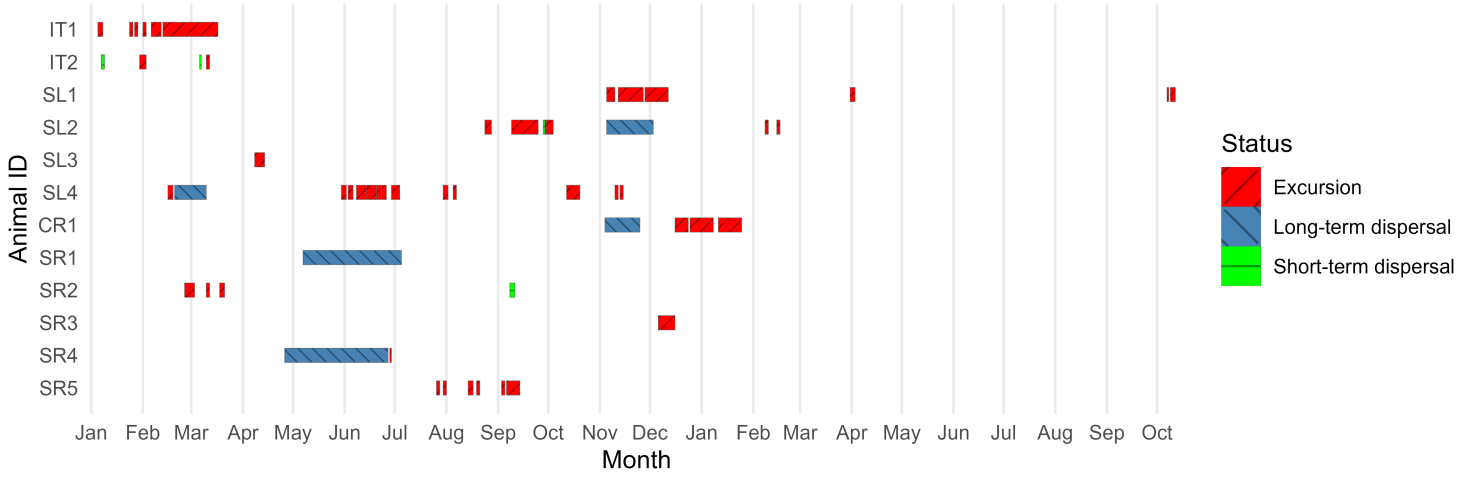

Figure 4

Occurrence and duration of excursions and dispersals of individual jackals throughout the tracking periods. Year length is extended onto the second calendar year to better represent chronological order of events.

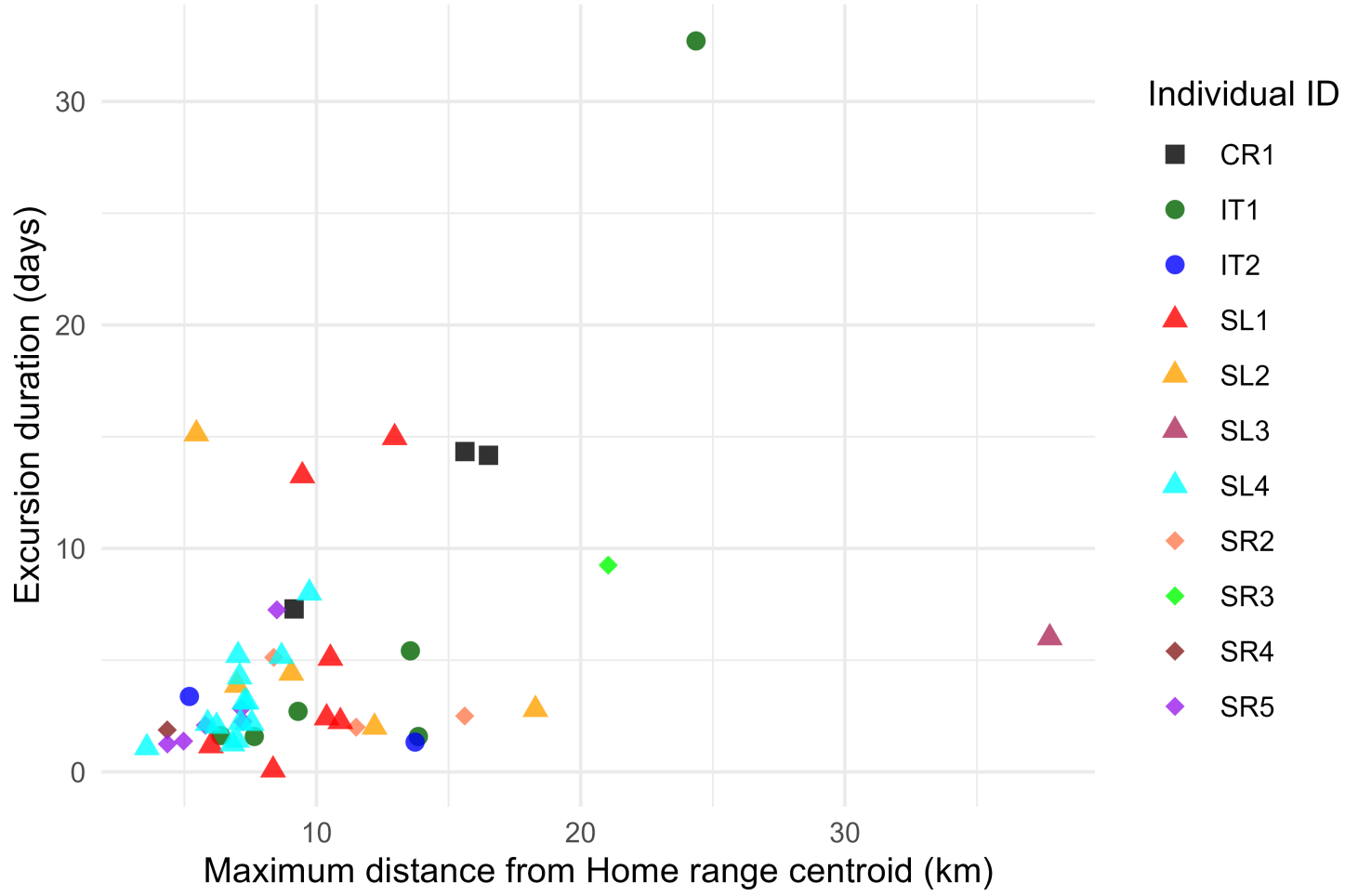

Figure 5

Distribution of excursions by distance from Home range and duration of movement

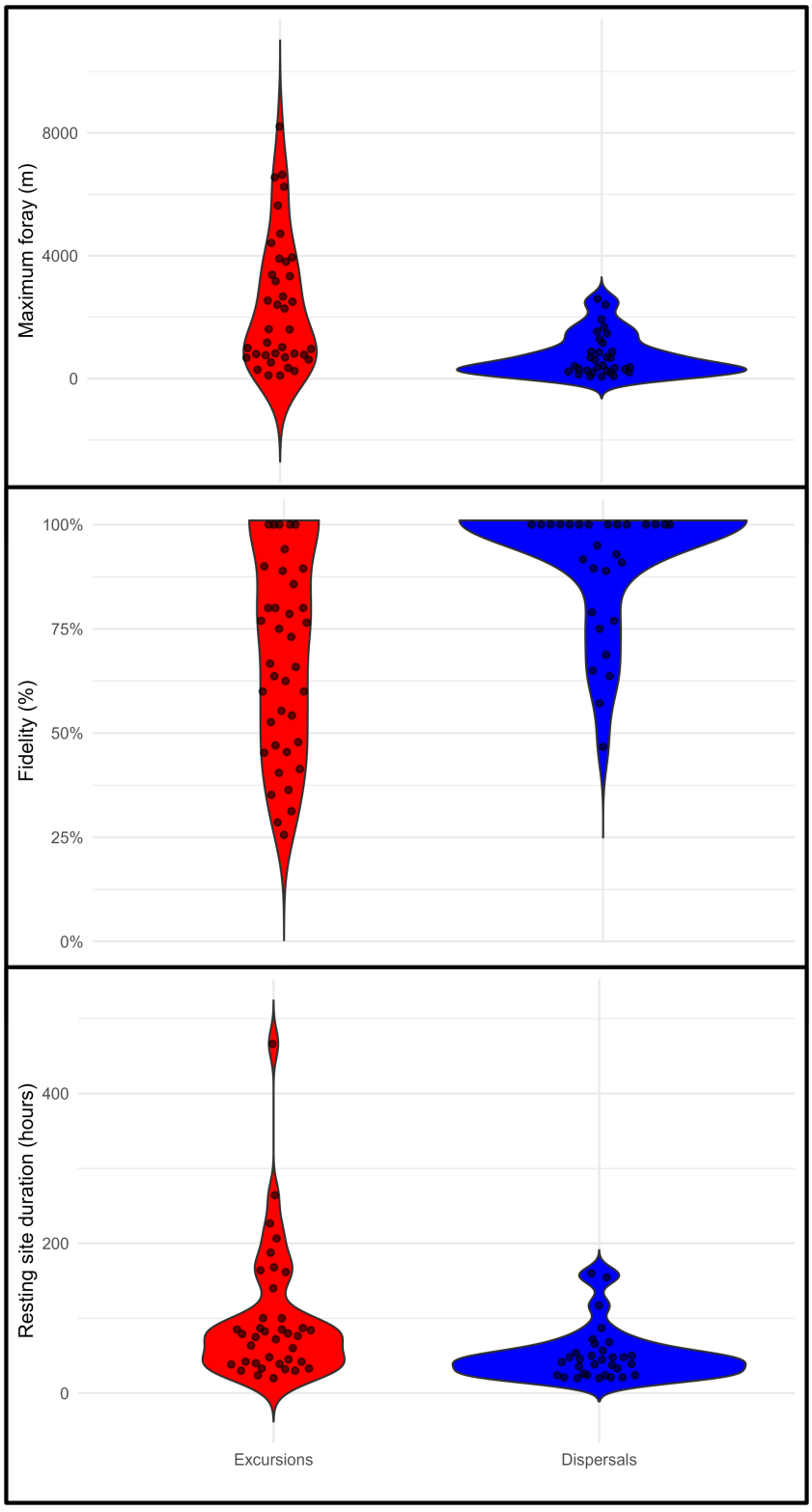

Figure 6

Distributions of resting site characteristics for excursion and dispersal resting sites: (a) resting site duration, (b) resting site fidelity, and (c) maximum forays per resting site. Violin plots show the full distributions with individual resting sites overlaid as points. Excursion resting sites are shown in red and dispersal resting sites in blue.

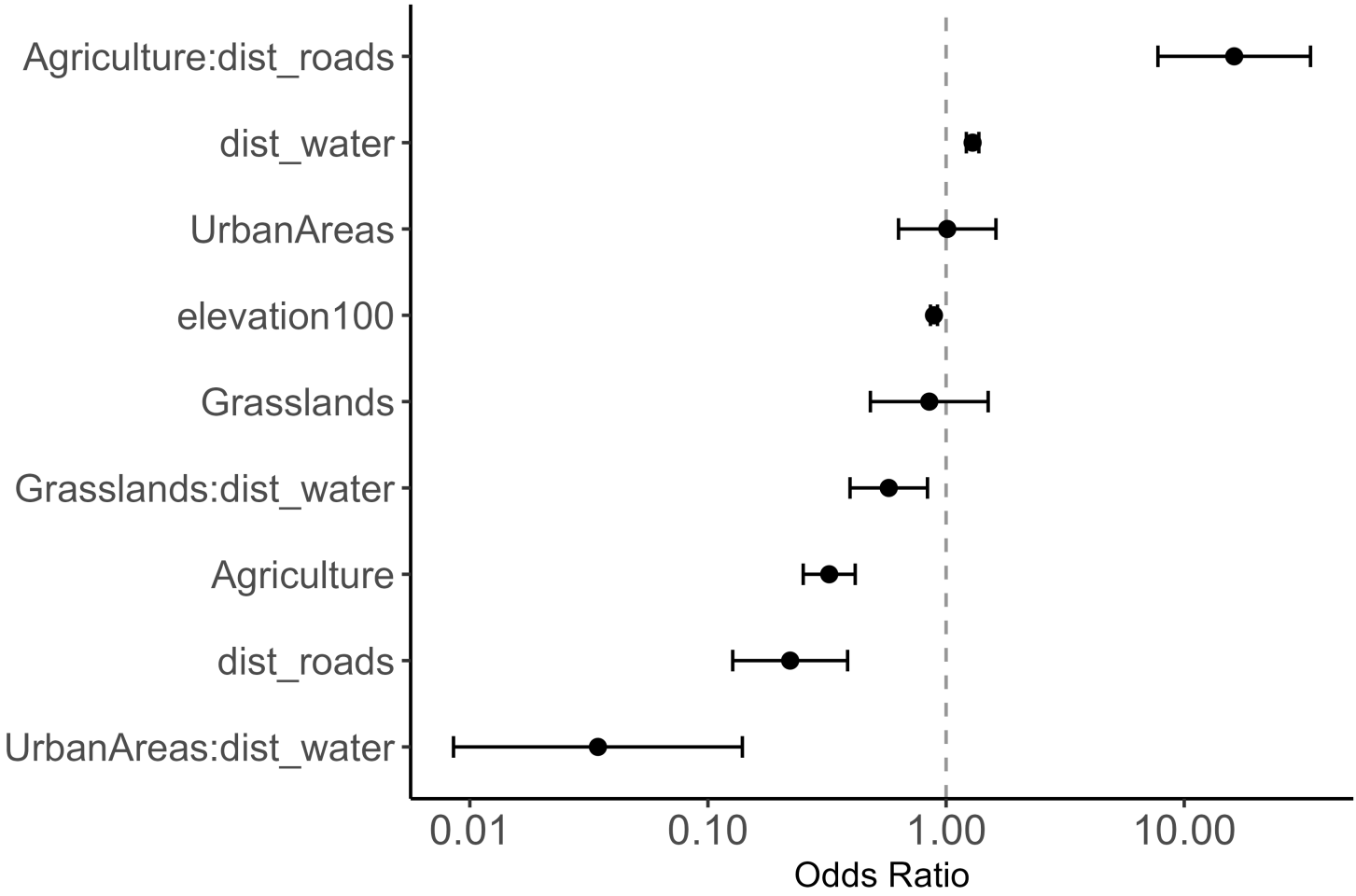

Figure 7

Odds ratios from the conditional logistic resting-site selection model. Values >1 indicate positive selection; values <1 indicate avoidance. Error bars denote 95% CIs; bars crossing 1 indicate insufficient evidence for selection. Elevation was scaled to 100 m difference, distance to water and to roads were in relation to 1 km.

Supplementary Files

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