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RESEARCH ARTICLE

Home ranges of roaming golden jackals in a European forest-agricultural landscape

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Abstract

The successful European expansion of the golden jackal (*Canis aureus*) is influenced by space use and an exploration of their movement ecology may promote the application of appropriate population management. However, little is known about their home range dynamics in forest–agricultural landscapes with dense populations and high hunting pressure. We evaluated home range size variations and movement patterns of golden jackals in southwestern Hungary, focusing on sex and age differences, seasonal variability, and the prevalence of irruptive nomad behavior. Over a 2-year study, we tracked 45 global positioning system (GPS)-collared jackals (22 females and 23 males) for an average of 245 days, collecting 236,675 hourly location points. We analyzed home ranges using the 95% kernel home range method, and used trajectory segmentation to identify residents (single home range) versus non-resident or irruptive nomads (multiple home ranges or home range shifts). Residents exhibited a mean (± SE) home range size of 14.38 ± 2.27 km^2 ($n = 28$), with significant individual variability (up to a 100-fold difference). Males had larger home ranges than females, and juveniles had larger home ranges than adults, particularly during pup-rearing periods. The home range shifts were more frequent for juveniles than adults, and females than males, whereas sex and age did not affect home range size of irruptive nomads (*n* = 17). Jackals mostly used forests close to forest–agricultural area edges and far from artificial structures. Our data revealed high interindividual space-use variability and intra-year differences in home range sizes between sexes, and substantiated the high ecological plasticity of this species. Our results likely relate to the complex social system of golden jackals along with a dense population, high hunting pressure, absence of large carnivores, and seasonal flexibility in response to abundant food sources.

KEYWORDS

Canis aureus, ecological flexibility, home range, population expansion, space-use analysis, trajectory segmentation

The golden jackal (*Canis aureus*) provides a recent example of significant mesopredator population growth in Europe, characterized by rapid expansion into new and historically uninhabited areas (Arnold et al. 2012, Rutkowski et al. 2015, Ranc et al. 2022, Stefanović et al. 2024). Their spread is similar to that of coyotes (*Canis latrans*) in North America (Crooks and Soulé 1999, Bekoff and Gese 2003, Gehrt et al. 2009). Like coyotes, many factors likely contributed to golden jackal expansion, such as the decline of large carnivores in the last century (Krofel et al. 2017, Newsome et al. 2017) and their opportunistic, generalist behavior (Hoffmann et al. 2018). Golden jackals have a flexible and complex social system consisting of a breeding pair, various non-breeding adults, and cubs (Macdonald et al. 2019; E. Csányi, University of Sopron, unpublished data). In these cooperative-breeding groups, females and males presumably share roles in pup-rearing and resource defense, while subordinate non-breeding adults (helpers) provide alloparental care (Macdonald et al. 2019). Their flexible diet allows them to exploit abundant food sources throughout Eurasia (Rotem et al. 2011, Lanszki et al. 2022). Furthermore, this species demonstrates long-distance dispersal (Lanszki et al. 2018*b*, Potočnik et al. 2019). Changes in climate and habitat that increase the availability of food resources have also been important factors in their expansion (Rather et al. 2020, Narang and Dutta 2022). The species' flexible movement ecology could promote successful expansion (Fenton et al. 2021, Kamler et al. 2021, Csányi et al. 2023).

Newly arriving or re-establishing species, such as golden jackals and coyotes, may substantially affect ecosystems (Crooks and Soulé 1999, Rotem et al. 2011, Ćirović et al. 2016, Balog et al. 2021). Clarifying the role of a species in the food web (Crooks and Soulé 1999, Glen et al. 2007) is necessary for mitigating existing human–wildlife conflicts (Trouwborst et al. 2015) in wild and domestic ungulate populations. Understanding how animals use space is essential for comprehending metapopulation dynamics and migration patterns (Jønsson et al. 2016, Narang and Dutta 2022), which aids in species and habitat conservation and population management (Allen and Singh 2016, Greggor et al. 2019). The reasons behind the rapid spread of the species and their potential impacts on Europe remain largely unknown but are assumed to influence ecosystem structure, biodiversity (Crooks and Soulé 1999, Morris and Letnic 2017, Cunze and Klimpel 2022), ecosystem services (Ćirović et al. 2016), and trophic interactions (Glen et al. 2007, Rotem et al. 2011, Kapota et al. 2016, Lanszki et al. 2018*a*). The distribution patterns and habitat use of golden jackals may directly influence their ecological impact; therefore, understanding these processes is essential.

Based on a geographic information system (GIS) analysis of European bio-acoustical jackal population survey data (Ranc et al. 2017), the probability of jackal presence was negatively associated with an increase in the human population and positively related to an increase in wetland coverage. The presence of jackals also showed a positive non-linear association with increased agricultural land. According to Tsunoda et al. (2018), jackals are expected to inhabit areas far from settlements. However, they are often seen close to water sources and frequently use agricultural areas and forests. The movement ecology of golden jackals has been studied using global positioning system (GPS) telemetry but only with a small sample in Europe (Hungary and Serbia, *n* = 5, Lanszki et al. 2018*b*, Fenton et al. 2021; Slovenia, $n = 1$, Potočnik et al. 2019; Italy, $n = 6$, Frangini et al. 2022*a*) and Asia (Thailand, $n = 2$, Charaspet et al. 2019, Jenks et al. 2015; Cambodia, $n = 3$, Kamler et al. 2021; India, $n = 7$, Katna et al. 2022). These limited data make it difficult to draw overarching conclusions.

For better understanding of the spatial ecology of golden jackals, larger sample sizes are necessary. By examining habitat use at the level of the home range, researchers can gain insights into how jackals respond to human influence, such as the availability of resources like food and shelter. This allows for assessment of the spatial patterns of movement and the ecological drivers behind their habitat use, ultimately informing better conservation and management strategies.

Using GPS tracking of golden jackals in a typical Central European forest–agricultural area, we investigated several aspects of their spatial ecology. Specifically, we examined 1) whether home range size varied depending on sex and age group and whether it changed during different biologically important periods (breeding, pup-rearing, and non-breeding), and 2) whether habitat-use characteristics (importance of resources) of resident and non-resident jackals differed at the home-range level based on how close they stayed to different land cover types (e.g., artificial surfaces, agricultural areas, forest). Following the resource dispersal hypothesis (Macdonald 1983, Carr and Macdonald 1986), we hypothesized that in a forest–agricultural (semi-natural) ecosystem, jackal home ranges would be large (Kamler et al. 2021) because of scattered but year-round available resources, including food, water, and shelter. We also hypothesized that home range sizes would vary (Ranc et al. 2017, Fenton et al. 2021, Kamler et al. 2021, Katna et al. 2022) based on seasonal reproduction, alloparental care, and high ecological plasticity. We predicted that compared to females males would have larger home range sizes (first prediction), that temporal variations would be considerable following the biologically important life stages of jackals (second prediction), that juveniles (1–2 years old) would more likely change their home range than older jackals (third prediction), and that home range shifts would correspond to differences in the use of habitats (fourth prediction).

STUDY AREA

We performed GPS collaring of golden jackals in the Pannonian biogeographical region of southwestern Hungary, Somogy County (Figure 1). The study area is part of the ecological network between Lake Balaton and the Dráva River. The northern part, where jackals were collared, belongs to the Boronka Landscape Protection Area near Nagybajom city (center: 46°27′ N, 17°27′ E). The middle and southern parts are around Segesd city (center: 46°21′ N, 17°18′ E) and Lábod village (center: 46°10′ N, 17°28′ E). This flat lowland area with dunes is situated 125–190 m above sea level and is dominated by forest–agricultural cover types.

Based on the location points of the 45 jackals, the 3,155-km^2 study area had relatively high forest coverage (45%), composed primarily of oak (*Quercus* spp.), willow (*Salix* spp.), alder (*Alnus* spp.), linden (*Tilia* spp.), and locust (*Robinia* spp.). Open agricultural lands (50%) mainly included arable lands with mostly sandy soil, primarily used for growing maize and cereals, such as wheat, triticale, oats, and rye, along with some grasslands. This area also contained wetlands (0.5%) and water bodies (1%). It is characterized by small settlements, with artificial structures making up 3%. The continental climate has sub-Mediterranean features, including moderately humid and mild winters, with an annual mean temperature of 10.3°C and precipitation of 700–750 mm (Lanszki et al. 2007, 2018*a*).

Red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), and wild boars (*Sus scrofa*) are important game species in this area. Hunting pressure on ungulates in the county is high by national standards (Somogy County: 5.4 individuals/km^2, Hungary, county mean ± SE: 4.3 ± 0.5 individuals/km^2; Csányi et al. 2022). High quantities of energetically profitable discarded viscera and hunted ungulate carcasses are the main foods of jackals (Lanszki et al. 2018*a*). The golden jackal is the largest predatory mammal in the area, and its population has grown considerably over the past 2 decades (Csányi et al. 2022). The jackal population density in this study (1.0 individuals/km^2; Csányi et al. 2023) and in this county can be considered high (hunting bag, Somogy County: 0.45 individuals/km^2, Hungary, county mean ± SE: 0.13 ± 0.03 individuals/km^2; Csányi et al. 2022) even in the Central

FIGURE 1 The study area with the tagging locations of the tracked golden jackals in a forest–agricultural ecosystem in southwestern Hungary in 2020–2023.

European context (Krofel et al. 2023). Jackal hunting is allowed year-round in Hungary without quota restrictions. Anthropogenic effects on the golden jackal population in the region, regarding both food availability and mortality from hunting, are significant (Csányi et al. 2023). The red fox (*Vulpes vulpes*) is the most common jackal competitor in the study area.

METHODS

Capture, data collection, and data processing

We captured golden jackals ($n = 45$) using baited box traps between 14 December 2020 and 6 January 2023 (Table S1). We used control poles and muzzles to immobilize captured animals without anesthesia and covered their heads with soft blankets during handling. We recorded body mass, body length, tail length, other morphological parameters, and age class for all captured jackals. We estimated age classes based on body dimensions, fur coloration, and dentition characteristics (Raychev et al. 1999). We classified 14 jackals as juveniles (>1 year but <2 years) and 31 as adults (≥2 years). We tagged captured jackals with Vertex Lite 1 C Iridium GPS satellite collars (Vectronic Aerospace GmbH, Berlin, Germany; collar weight = 270 g; mean accuracy = 8–15 m). We identified jackals according to sex and capture order (e.g., ID codes F1 and M1; Table S1, available in Supporting Information). We captured animals according to Hungarian legislation on hunting and with relevant authorization (permission number SO/FM/02856-1/2020).

We downloaded data from the GPS collars via the Vectronic INVENTA wildlife monitoring web service or upon recovery. We recorded 236,675 location points (males: $n = 122{,}638$; females: $n = 114{,}037$) for 45 GPS-collared jackals between December 2020 and January 2023. The proportion of missing data, based on the possible 24 daily positions, was 4.6%. We tracked the animals for a mean (±SE) of 244 ± 15 days (80–416 days). Messages containing 12 fixes were transmitted via a 2-way Iridium satellite long-range communication system. Based on speed and distance calculations combined with visual verification, we filtered out 6 location points classified as outliers with the ctmm package (Calabrese et al. 2016) in R (version 4.2.3; R Core Team 2020).

Data analysis

We analyzed the data of 22 female and 23 male jackals during the study period. To analyze the GPS location data, we divided the study period into seasons based on biologically important life stages of the jackal, according to Giannatos (2004), the expert surveyors' experience, and our previous camera trap records. The periods were 1) breeding (mating and pregnancy; Jan–Mar), 2) pup-rearing (when pups are dependent on parental care; Apr–Jun), and 3) the non-breeding period (Jul–Dec).

We calculated home range size by different methods, namely 95% kernel home range (KHR; Worton 1989), alpha concave hull (ACH; Asaeedi et al. 2017), and 95% autocorrelated kernel density estimations (AKDE; Fleming et al. 2015) with statistical models (Tables S1, S2, available in Supporting Information). Ultimately, KHR provided the most consistent results and was the least sensitive to special point patterns; therefore, we chose this estimation method for our further analyses. We conducted KHR analyses using the adehabitatHR package (Calenge 2006) in R.

We classified the tracked jackals as residents or non-residents (irruptive nomads) based on their space-use patterns observed during the study period. We considered jackals to be residents if they remained within a single, definable home range throughout the study period and irruptive nomads if they occupied several separate home ranges (shifted their previous home range). Irruptive nomadism is a form of nomadic movement where long-distance movement events are unpredictable in their timing and direction but may be interspersed by relatively long periods of residency (Teitelbaum and Mueller 2019).

To identify these 2 groups, we used trajectory segmentation analysis in R with the adehabitatLT package (Figures S1, S2, available in Supporting Information). We re-discretized the individuals' trajectories to 1-hour intervals to interpolate missing locations. We then applied Lavielle segmentation (Lavielle 1999; minimum number of observations per segment = 48, with the mean as the path signal parameter and net squared displacement as a parameter to identify dispersal movements) to determine the optimal number of segments. By graphically examining the decreasing trend of the contrast function, we used the number of segments where clear breaks could be found on the slope. When no break was present, we categorized jackals as residents regardless of their home range size. When multiple breaks were present (e.g., F02), we determined the optimal number by visually comparing the potential number of segments and selecting the one with the least spatial overlap among segments. We considered the distance between home range centroids of different segments to be the dispersion distance (Kojola et al. 2006). We calculated centroids as the arithmetic mean values of the longitude and latitude coordinates (KHR) and direction angles as the difference from the north direction using the bearing() function of the sf package (Pebesma 2018) in R.

To explain variation in home range size, we fit generalized linear mixed models (GLMM) using the lmer function from the lmerTest package (version 3.1.3; Kuznetsova et al. 2017) in R version 4.4.1 (R Core Team 2020) in 2 sets. The first set was based on the data of resident jackals ($n = 28$ jackals), and the second was on irruptive nomads ($n = 17$ jackals). Home range size, calculated using the KHR method with log $(1 + x)$ transformation, was the response variable. In the first model, we used the following fixed effects as explanatory variables: sex, age group, and period (3 periods) to investigate the intraspecific variability within the resident group. In the second model, we used sex, age group, and home range sequence (consecutive home ranges) to detect factors affecting home range shift of irruptive nomads. We included the ID of jackals as a random factor in all models. We excluded periods with fewer than 135 location points for the home range size calculation ($n = 10$ cases). The full models included the aforementioned explanatory variables (fixed effects) and their pairwise interactions. To select the final models, we used the step function from the lmerTest package with backward selection. We applied log transformation to normalize the residuals, and we checked the model fit on QQ plots.

To evaluate habitat use (i.e., how much are habitat feature edges used) of the tracked individuals, we used the basic level land cover categories (artificial surfaces, agricultural areas, forest and semi-natural areas, wetlands, and water bodies) from the Corine Land Cover 2018 dataset (©Copernicus Program; created with the support of the European Union). These categories were grouped into 5 land cover types or features: forests, open agricultural lands, artificial structures, wetlands, and water bodies. We calculated distances to the nearest land cover feature (patch) in meters for all location points. We determined the land cover composition within the area used by the jackals based on the buffered (10 km) convex polygon, considering all location points of the 45 individuals. We used the same area to demonstrate the distance zones between the network of settlements and water bodies in the study area.

To test whether distance values differed between resident and non-resident jackals, we first randomly selected 500 samples of all GPS location points from within each land cover category and resident versus non-resident grouping, using the dplyer package (Wickham et al. 2024) in R software (random seed = 123). We then used a 2-way permutational multivariate analysis of variance (2-way PERMANOVA; 9,999 random permutations) with movement form (2 categories: resident or non-resident) or land cover category (5 categories) as independent factors. Similarity percentage (SIMPER) analysis highlighted which land cover categories contributed most to the dissimilarity in habitat use between resident and non-resident jackal groups. The PERMANOVA and SIMPER results were based on Bray–Curtis dissimilarity matrices (PAST software version 4.1; Hammer et al. 2001). We performed a similar stratified sampling and analysis procedure for non-resident jackals to test whether the distance to landscape features differed between the periods before and after a home range shift (500 random samples for each).

For data visualization, we used R software with the ggplot2 package (Wickham 2016). For spatial data visualization and distance calculation, we used QGIS software version 3.16 (QGIS Development Team 2023) and the Serval plug-in (Pasiok 2019).

RESULTS

Space-use patterns of resident jackals

The mean (±SE) home range size of the 28 resident jackals was 14.38 ± 2.27 km^2 (Table 1). Home range size was markedly influenced by sex, age group, and period (Table 2). The home range of males was larger than that of females

TABLE 1 Home range sizes of resident golden jackals grouped by sex, age, and period in southwestern Hungary, 2020–2023, based on 95% kernel home range methods.

Groups	*n*	Mean	SE	95% CI	Range
Females	31	7.40	0.85	5.68–9.13	1.74–23.22
Males	44	19.29	3.66	11.91–26.67	1.06–106.83
Juveniles	16	14.76	5.07	3.96–25.56	1.74–66.59
Adults	59	14.27	2.56	9.15–19.39	1.06–106.83
Breeding period	16	11.24	3.84	3.06–19.43	1.06–63.31
Pup-rearing period	31	17.18	4.69	7.60–26.76	1.74–106.83
Non-breeding period	28	13.07	2.33	8.29–17.84	2.61–54.31
All	75	14.38	2.27	9.86–18.90	1.06–106.83

TABLE 2 Results of a generalized linear mixed-effect model of resident jackals' home range size in southwestern Hungary, 2020–2023, based on 95% kernel home range methods.

Effect	Estimate	SE	*t*	*P*(>|*t*|)
(Intercept)	6.761	1.377	4.912	<0.001
Sex	−0.494	0.187	−2.636	0.015
Age group	−2.199	0.722	−3.047	0.003
Period	−1.622	0.563	−2.880	0.005
Age group × period	0.960	0.303	3.174	0.002

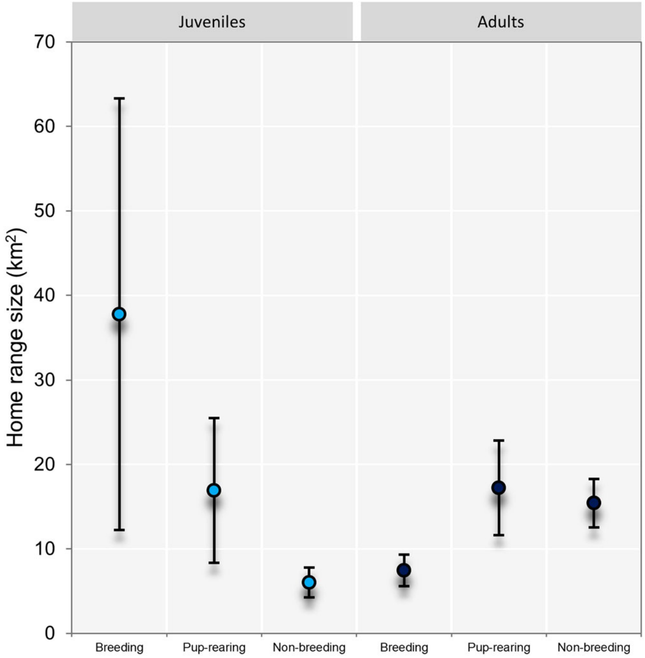

FIGURE 2 Home range sizes (mean ± SE) of resident juvenile and adult golden jackals in different periods in southwestern Hungary, 2020–2023, based on the 95% kernel home range calculation method.

(mean = 19.29 km^2 vs. 7.4 km^2, $P = 0.015$). Juveniles used larger home ranges than adults (mean = 14.76 km^2 vs. 14.27 km^2, $P = 0.003$), and jackals expanded their home range during the pup-rearing period (mean = 17.18 km^2) compared to the breeding (11.24 km^2) and non-breeding period (13.07 km^2; $P = 0.005$). The age group × period interaction ($P = 0.002$) indicated that mean home range size of juveniles was largest during the breeding period (37.78 km^2) and then decreased, whereas that of adults was largest during the pup-rearing period (17.25 km^2; Figure 2). The R^2 explained by the fixed effects was 0.213, while the R^2 for the full model was 0.238. The intraclass correlation coefficient (ICC) was 0.032. During the study period, some resident jackals of both sexes increased or extended their home range (mostly males; e.g., M10, M06, M17, M01, M16, M07, M02, M09, and F17), narrowed it (e.g., F20, F12, F06, M03, M07, and M13), or displaced the center of their movement within the home range (mostly females; e.g., F22, F21, F03, F13, and M22), although none of these displacements was particularly large (Figure S1, Animation S1, available in Supporting Information).

Space-use patterns of non-resident jackals

Of the 45 jackals, half of the juveniles (7/14), nearly a third of the adults (10/31), half of the females (11/22), and almost a quarter of the males (6/23) were classified as irruptive nomads. Based on trajectory segmentation analysis of those 17 jackals, 13 individuals (76.5%) changed their home range once, and 4 changed their home range twice (23.5%; Figure S2, available in Supporting Information). The mean (±SE) home range size of the irruptive nomad jackals was 92.44 ± 20.59 km^2 (Table 3). The home range size was not influenced by sex and age group but depended on the home range sequence (Table 4), with the largest size in the third home range (mean third home range = 185.26 km^2, first home range = 83.41 km^2, second home range = 79.64 km^2; $P < 0.001$). There was strong evidence supporting sex × home range sequence and the age group × home range sequence interactions. The home range size of males did not change among sequences (mean = 37.16–59.43 km^2); the home range size of females was larger after the second home range shift (mean third home range = 333.37 km^2, first home range = 96.4 km^2, and second home range = 100.40 km^2; $P = 0.003$; Figure 3A). The home range of juveniles decreased, while that of the adults increased during home range changes ($P = 0.001$; Figure 3B). The R^2 for the fixed effects was 0.223, and for the full model, it was 0.779; the ICC was 0.716.

The mean (±SE) dispersal distance of jackals based on the distance between home range centroids, was 14.37 ± 2.72 km, ranging between 1.46 km and 56.43 km, and the displacements were directed in many directions

TABLE 3 Home range sizes of irruptive nomad golden jackals grouped by sex, age, and home range sequence in southwestern Hungary, 2020–2023, based on 95% kernel home range methods.

Groups	*n*	Mean	SE	95% CI	Range
Females	24	118.02	30.78	54.35–181.70	3.29–637.86
Males	14	48.59	12.94	20.63–76.56	3.18–184.69
Juveniles	15	66.45	26.90	8.75–124.15	3.18–409.51
Adults	23	109.40	29.06	49.12–169.67	3.29–637.86
First home range	17	83.41	22.75	35.17–131.64	3.29–409.51
Second home range	17	79.64	22.92	31.06–128.22	3.18–263.44
Third home range	4	185.26	151.06	n.a.–666.01[a]	18.91–637.86
All	38	92.44	20.59	50.72–134.16	3.18–637.86

[a] n.a. = not applicable (negative value).

TABLE 4 Results of a generalized linear mixed-effect model of irruptive nomad jackals' home range size in southwestern Hungary, 2020–2023, based on 95% kernel home range methods.

Effect	Estimate	SE	*t*	*P*(>|*t*|)
(Intercept)	9.052	1.938	4.671	<0.001
Sex	−1.380	0.842	−1.639	0.111
Age group	−1.676	0.836	−2.004	0.054
Home range sequence	−4.538	0.935	−4.856	<0.001
Sex × home range sequence	1.239	0.363	3.413	0.003
Age group × home range sequence	1.407	0.376	3.739	0.001

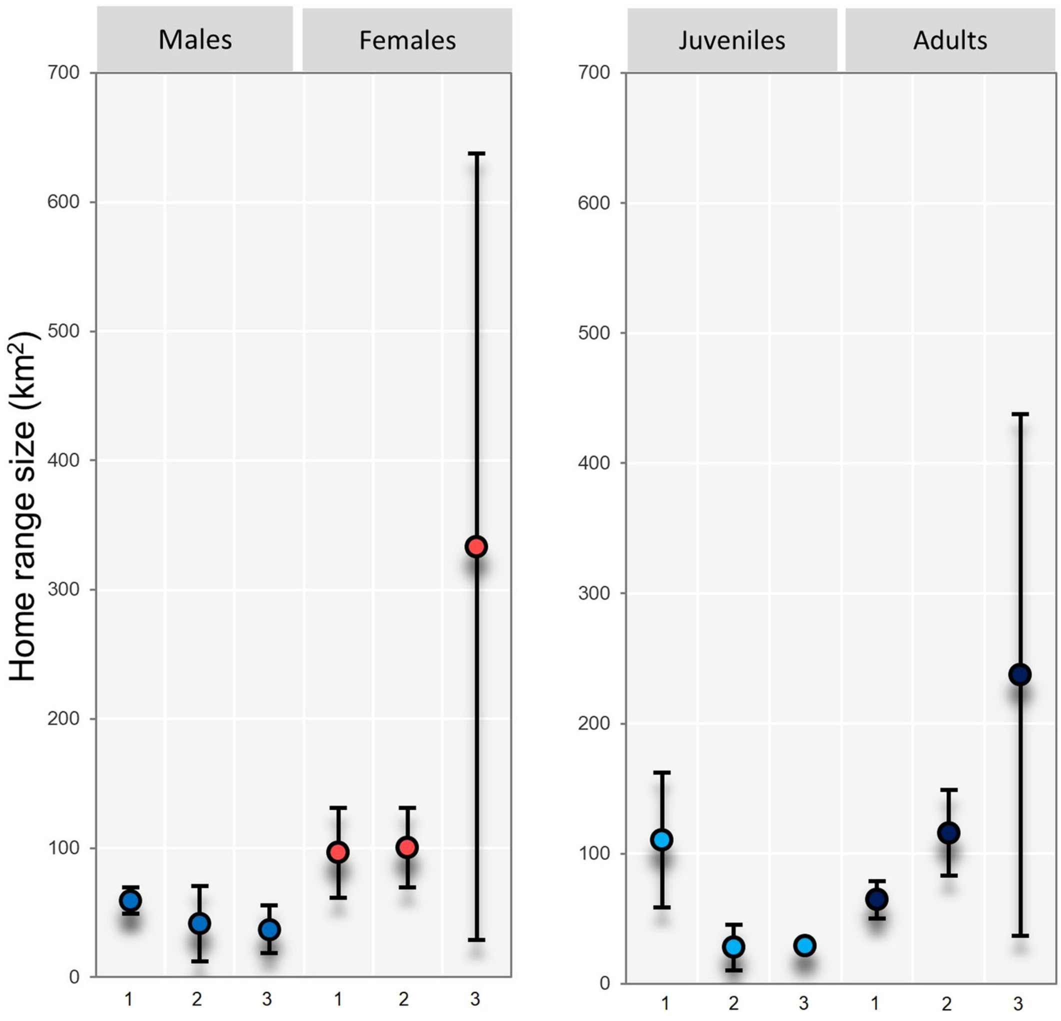

FIGURE 3 First (1), second (2), and third (3) home range sizes (mean ± SE) of non-resident (irruptive nomad) golden jackals depending on sex and age group in southwestern Hungary, 2020–2023, based on the 95% kernel home range calculation method.

(Figure S3, available in Supporting Information). Home range shift occurred during all 3 biologically important periods (Figure S4, available in Supporting Information): breeding (3 shifts by females and 3 by males), pup-rearing (2 shifts by females and 3 by males), and non-breeding periods (8 shifts by females and 2 by males).

Distance to landscape feature edge

The location points of collared jackals ($n = 45$ jackals, 5,258 ± 342 SE points/jackal) were recorded close to the edges of forest–agricultural areas, namely inside the forest ($\overline{x}$ = −294 m; range = −3,135 to 2,569 m) and outside in the field ($\overline{x}$ = 397 m; range = −1,586 to 3,239 m; negative values represent locations within the given land cover category), while they were located relatively far from artificial structures ($\overline{x}$ = 3,147 m; range = −184 to 6,006 m), wetlands ($\overline{x}$ = 7,221; range = −494 to 13,662 m), and water bodies ($\overline{x}$ = 3,886 m; range = −2,032 to 12,751 m; Figure 4).

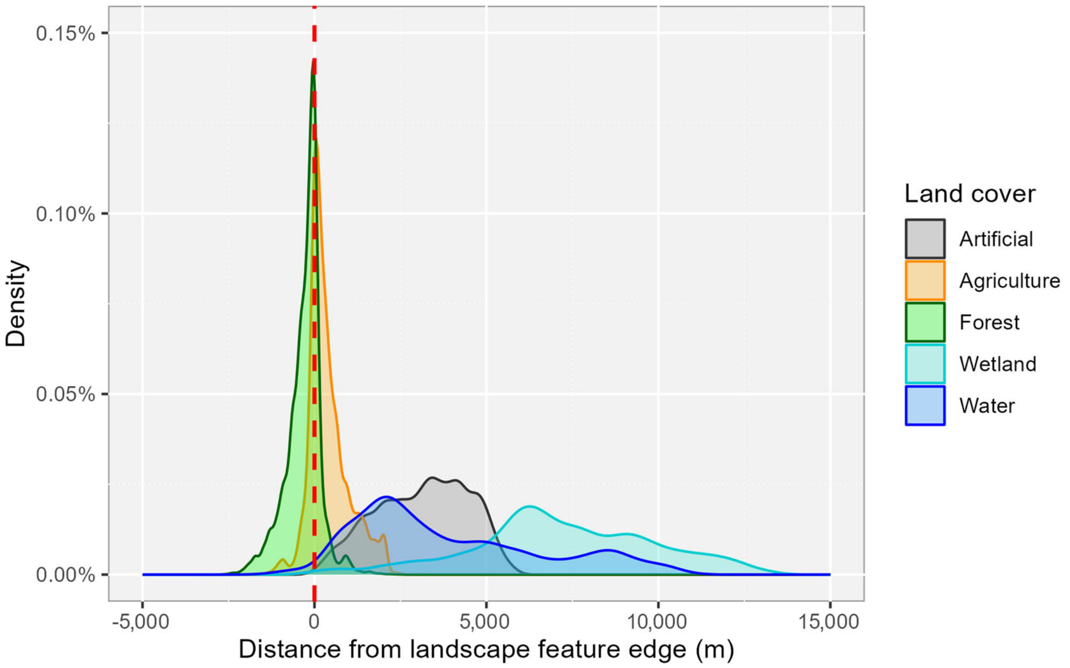

FIGURE 4 Distribution of the distance of golden jackal locations ($n = 45$ jackals; 236,675 locations) from landscape feature edges, southwestern Hungary, 2020–2023. The red dashed line represents the edge of the landscape features while negative values represent locations within them.

Based on the 2-way PERMANOVA analysis, the distances to distinct landscape feature edges differed between residents and non-residents (2-way PERMANOVA for movement form × land cover category, $F_4 = 800.55$, $P < 0.001$). The distances did not differ depending only on the groups (resident vs. non-resident; $F_2 = -3{,}015.1$, $P = 1.00$) but differed depending on only land cover categories ($F_4 = 2{,}063.2$, $P < 0.001$). The SIMPER analysis showed that wetlands accounted for 36.3%, water bodies accounted for 32.7%, and artificial surfaces accounted for 18.3% of this difference (Table S3, available in Supporting Information). While both groups stayed close to forest–agriculture edges, non-residents moved closer to artificial structures and wetlands and farther away from water bodies than residents (Figure 5; Figure S5, available in Supporting Information).

For irruptive nomad jackals, distances to landscape feature edges differed before and after their home range shift (2-way PERMANOVA for home range shift × land cover category, $F_4 = 422.39$, $P = 0.003$). Distances did not differ depending only on the home range shift ($F_1 = -135.89$, $P = 0.723$) but did differ depending on only land cover categories ($F_4 = 477.26$, $P < 0.001$). Wetlands accounted for 40.0%, water bodies accounted for 32.8%, and artificial surfaces accounted for 6.8% of this difference (Table S4, available in Supporting Information). While in both cases the jackals stayed close to forest–agriculture edges, they moved farther from artificial structures and wetlands and closer to water bodies after their home range shift than before (Figure 6).

DISCUSSION

This study represents the first analysis of home range size for golden jackals in central Europe based on satellite GPS tracking of multiple animals within a single region with frequent (hourly) measurements. The resulting patterns, which we could only assume previously from some telemetry studies and field observations carried out on a smaller

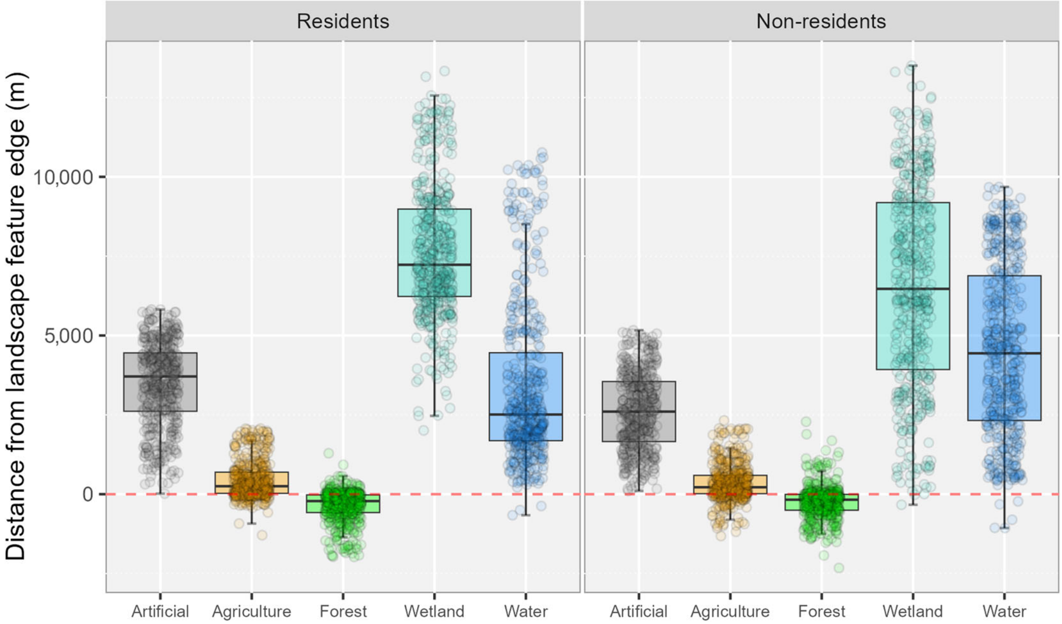

FIGURE 5 Distance of locations of resident and non-resident (irruptive nomad) jackals from landscape feature edges, southwestern Hungary, 2020–2023. The lower and upper hinges correspond to the 25th and 75th percentiles (quartiles). The whiskers extend from the lower and upper hinges to the 1.5× inter-quartile ranges.

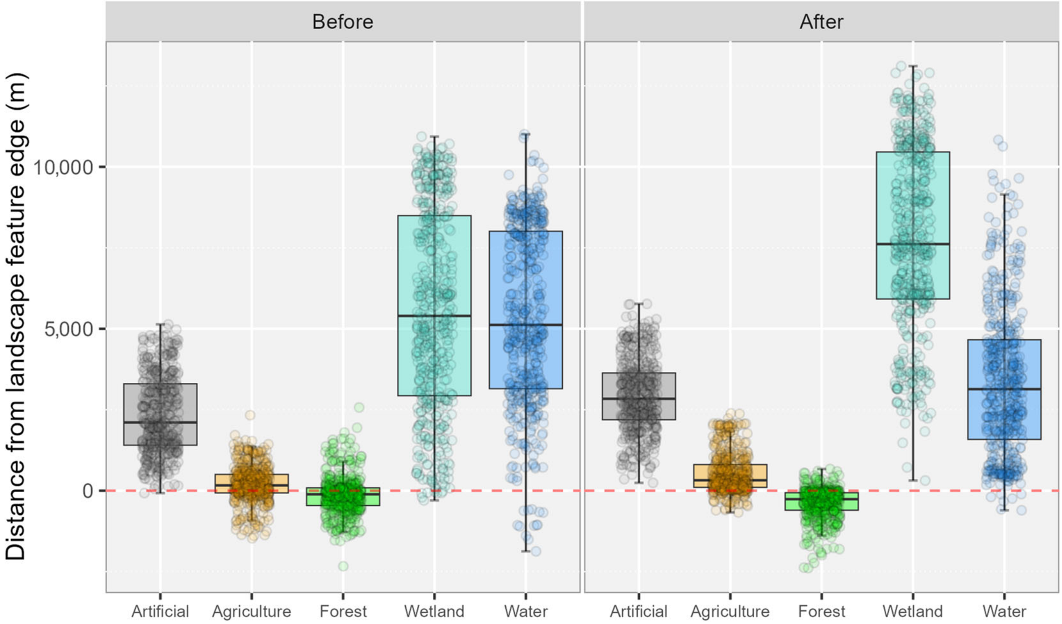

FIGURE 6 Distance of locations of non-resident (irruptive nomad) jackals before and after home range shift from landscape feature edges, southwestern Hungary, 2020–2023.

number of individuals, may typify the spatial ecology of the central European golden jackal population. This is significant as jackals are expanding westward and northward, making their spatial characteristics in Hungary potentially indicative of the species' expansion across Europe (Rutkowski et al. 2015, Stronen et al. 2021).

The home range size of golden jackals is large and variable

As expected, the estimated home range sizes of golden jackals in our forest–agricultural area were large and varied widely. Regardless of the calculation method (Table S1), mean home range values for resident jackals were similar to those observed in natural areas of Asia (Aiyaduari and Jhala 2006, Kamler et al. 2021) but larger than those found in central and southeastern Europe (Giannatos 2004, Fenton et al. 2021, Frangini et al. 2022*a*). For some resident jackals in our study (e.g., M01, M06, M07, M13, and M24; Table S1), home range size was similar to the highest values recorded by Aiyadurai and Jhala (2006) in India (95% KHR = 7.24–77.22 km^2) and at the edge of the jackal population in Cambodia (95% KHR = 40.1–50.8 km^2; Kamler et al. 2021). Furthermore, our home range sizes were consistent with those of resident mesocanid species studied in Eurasia, Africa, and North America (coyote: Schrecengost et al. 2009, Mastro et al. 2019; black-backed jackal [*Canis mesomelas*]: Kamler et al. 2019; golden jackal: Moehlman and Hayssen 2018, Kamler et al. 2021).

Previous studies using telemetry on jackals in Asia have supported the flexible space use of jackals. Kamler et al. (2021) reported particularly small home ranges, with wide variations from 0.1 km^2 to 14.3 km^2 (143-fold difference) in agricultural areas near settlements and anthropogenic food sources, whereas in less populated areas, they observed more extensive home ranges (21.2–47.1 km^2). In Europe, Fenton et al. (2021) reported a home range of 11.2 km^2 (90% AKDE) and a core area of 2.4 km^2 (50% AKDE) based on 6 GPS-collared golden jackals in Hungary and Serbia. Giannatos (2004) reported home range sizes ranging from 2.2 km^2 to 15 km^2 (6.8-fold difference) using convex polygons for 3 radio-tracked (very high frequency) jackals. In our study, in a sparsely populated forest–agricultural area, the differences between the smallest and largest home range values of the 28 resident jackals were 100-fold, while those of the 17 irruptive nomads varied 200-fold. The mean home range sizes of irruptive nomads were 6.45 times that of resident jackals.

The extensive variation in home range sizes observed among golden jackals in this study was likely influenced by the diversity of land cover types and richness of food sources. Forested areas with hunted populations of big game species contribute resources such as viscera, carcasses, and wounded animals easily accessible to jackals year-round. Additionally, periodic peaks in rodent populations in forests and arable land contribute to the richness of available food (Lanszki et al. 2007, 2018*a*). Abundant food and favorable habitat conditions typically lead to smaller home ranges in less social carnivores (Kamler and Gipson 2000, Macdonald et al. 2019, Kamler et al. 2021). However, our study reveals that even in the rich habitats of our study area, alloparental jackals use relatively larger areas. The large and variable home range values we observed may have stemmed in part from a dense jackal population (minimum of 1 jackal/km^2), which exceeds densities seen in other European studies (Krofel et al. 2023). Factors such as food availability, diverse foraging opportunities (Ćirović et al. 2016), and human activities like sport hunting of jackals (Csányi et al. 2022) likely influence instability in home ranges. Intensive hunting permanently damages the family structure in canids (Glen et al. 2007, Csányi et al. 2023), which can presumably cause a variable dispersion distance in a high-density jackal population.

The home range size of residents depends on sex, age, and biological period

Supporting our first prediction, male jackals exhibited home ranges 2.6 times larger than females, a common trend observed in many carnivores (Gehrt et al. 2009, Simcharoen et al. 2014, Karelus et al. 2021). Golden jackal males are larger in body size than females (Csányi, Sándor 2024). In individual cases, the jackal pair uses the same home range together (Fenton et al. 2021, Csányi et al. 2023), but we lacked the ability to track pairs of jackals in this study. The intrasexual variability we observed may be due to both breeding and non-breeding females being collared (Giannatos 2004).

Supporting our second prediction, the largest mean home range was observed during the pup-rearing period, but age group influenced period-dependent patterns. Juveniles had the largest home range size during the breeding period, while adult home ranges were largest during the pup-rearing period. The difference between age groups is presumably due to variations in reproductive status, with the majority of juvenile (1–2 years, sexually mature) individuals likely serving as helpers, as found in closely related canid species (Moehlman 1987, Macdonald et al. 2019). The breeding season (mating and pregnancy; Jan–Mar) of jackals coincides with intensive hunting of big game species, providing large amounts of big game viscera and carcasses for scavengers in the area (Lanszki et al. 2018*a*). Consequently, jackals likely spent less time searching for food during the breeding season, as reflected by the similar, relatively small home range values independent of sex and in the adult age group during that period.

During the pup-rearing period, the nutritional needs of pups requiring parental care gradually increase (Mukherjee et al. 2018, Kamler et al. 2021). Coinciding with spring and early summer (Apr–Jun), food sources (fruits, small mammals) or accessibility (big game species viscera and carcasses) may be more limiting for jackals. These factors can result in a larger home range size. According to the resource dispersal hypothesis (Macdonald 1983), changes in group size can affect home range size. For example, in gray wolf (*Canis lupus*) in Poland, males were less active and mobile during the mating season when the pack size was larger compared to when the pack consisted only of the breeding pair (Tsunoda et al. 2009). Thus, the roles of the mating males and pup-rearing females likely affect the individual's activity, and alpha males in larger packs move less during the pup-rearing period because they are assisted by other pack members (Ciucci et al. 1997, Tsunoda et al. 2009). Intensive hunting in the area may also affect home range size through the family structure (Csányi et al. 2023). Vacant territories may soon be occupied by juvenile or adult jackals.

The ripening of fruits in summer and autumn and sport hunting of ungulates in autumn and winter provide ample and easily accessible food for all age classes, contributing to smaller home range sizes in the non-breeding period (Jul–Dec). During this period, mesocanid pups learn to hunt and join their parents and helpers in feeding and acoustic communication (Moehlman 1987). This period is also the time of dispersal (Lanszki et al. 2018*b*, Potočnik et al. 2019), but this was not clear in the case of the European golden jackal, and we observed dispersal to occur in nearly every month of the year.

Factors affecting the space use of non-resident jackals

According to the individual-fitness-based theory (Moehlman 1987, Macdonald and Carr 1989), juvenile (or sub-adult) mesocanids may choose to forgo mating and stay with their parents for another 6–8 months to help raise new pups or leave the natal territory to raise offspring. They face the same choice at the end of the next breeding period (Moehlman 1987). Golden jackals and African golden wolves (*Canis anthus*; Koepfli et al. 2015) are sexually mature at 1 year of age (Macdonald 1979, Moehlman 1987, Giannatos 2004). In gray wolves, 10–12-month-old individuals of both sexes disperse (Gese and Mech 1991, Kojola et al. 2006). Juvenile (sexually mature) mesocanid males are less likely to stay with the breeding pair and have a higher dispersal rate (Moehlman 1987, Rotem et al. 2011, Kapota et al. 2016, Zepeda et al. 2021).

As expected, in our study juvenile jackals shifted their home range more frequently than adults (50% vs. 31%), with the relatively high proportion of irruptive nomads in the adult group related potentially to a breakdown of the family structure due to intensive hunting in the area (Csányi et al. 2023). In contrast to expectations, we found that female jackals shifted their home range twice as often as male jackals (50% vs. 23.6%), a pattern similar to the Ethiopian wolf (*Canis simensis*; Sillero-Zubiri et al. 2004). The higher rate of home range shift in female jackals may also relate to an often-broken social system (e.g., intense hunting pressure or killed females), as seen in dingoes

(*Canis lupus dingo*; Glen et al. 2007), leading them to immediately try to fill a newly vacant breeding position (Csányi et al. 2023). Observed home range shifts occurred over a relatively short distance (mean = 14.4 km), presumably directed to the territory of neighboring or nearby groups. The distance between home range centroids of 6 individuals was >20 km, with one moving extremely far, at 56.4 km (F19 jackal). This pattern is similar to that observed in coyotes, whose dispersal may occur in vacant or occupied territories adjacent to the natal territory or over long distances (Gese and Bekoff 2004).

Home range shifts occurred year-round, independently of biologically important periods. Contrary to our third prediction, sex and age did not influence differences in home range patterns before and after the initial home range shift. However, interactions indicated the presence of sex and age influences, primarily resulting from individual cases. Some irruptive nomad adult golden jackals used vast spaces (F01 jackal, 638 km^2), a size characteristic of the gray wolf in northern latitudes (Okarma et al. 1998, Mech and Boitani 2003) and much larger than that measured in the Balkans (100% minimum convex polygon of packs = 141 km^2 and 160 km^2; Kusak et al. 2005). Dispersal of coyotes typically occurs during autumn and early winter (Gese et al. 1996), and in wolves, it peaks in autumn and spring (Gese and Mech 1991, Kojola et al. 2006). Dispersal in the European golden jackal population has been observed earlier in December and January (Lanszki et al. 2018*b*, Potočnik et al. 2019). Nonetheless, home range shifts can also occur in summer (Csányi et al. 2023) by applying the strategy of staying and waiting for a vacancy regarding either territory or mate (Moehlman 1987, Mech and Boitani 2003, Glen et al. 2007, Sparkman et al. 2011, Morin and Kelly 2017).

Non-resident jackals moved closer to settlements than residents

Habitat selection of the golden jackal in Europe remains poorly understood, with limited studies addressing this topic (Giannatos 2004, Šálek et al. 2014, Ranc et al. 2017, Frangini et al. 2022*b*). Without a detailed analysis of habitat use, predicting their behavioral response is challenging. We aimed to enhance understanding of their home range by examining the distance from habitat edges. In our study, similar patterns could be found in both resident and irruptive nomad jackals regarding the distances from forest and agriculture, but at the same time, we observed slight differences in the case of artificial surfaces, wetlands, and water bodies. Similarly, we observed slight differences in the case of those land cover types among non-residents before and after home range shifts.

Human proximity is considered risky for carnivores (Kusak et al. 2005), particularly under conditions of intensive hunting (Glen et al. 2007, Csányi et al. 2023), as is observed in our study location. Simultaneously, the abundance of food sources associated with human activities may be attractive to jackals (Macdonald 1979, Rotem et al. 2011, Kapota et al. 2016, Kamler et al. 2021). In our study, jackals stayed as far away from settlements as possible (Figure S5), with only irruptive nomads occasionally venturing closer, especially before their home range shifts.

Irruptive nomad jackals tended to be closer to artificial structures and farther from water bodies than residents, with their data showing more variability. Irruptive nomad individuals may be subordinate (Moehlman 1987, Hinton et al. 2015) because they are weaker, forced out of prime habitats, or more adventurous and exploring less-preferred jackal habitats (Hinton et al. 2016, Frangini et al. 2022*b*). Based on the behavioral characteristics of social canids (Giannatos 2004, Kusak et al. 2005, Ranc et al. 2017), we initially assumed that the proximity of surface water bodies would be important for jackals. Yet compared to the dominance of forest–agricultural areas, wetlands and water bodies were relatively sparse and small scale in our study area (Figure S5). Often, aquatic features did not fall within the home ranges of individual jackals or were located only on home range edges, potentially serving as natural territory boundaries (Csányi et al. 2023). The location of irruptive nomad jackals farther from water bodies suggests that residents may better monopolize water resources. Overall, water does not appear to be a limiting factor in the area, and jackals can persist in semi-desert conditions (Hoffmann et al. 2018).

MANAGEMENT AND RESEARCH IMPLICATIONS

We observed large and highly variable home range sizes, frequent home range shifts, and a high proportion of irruptive nomads among golden jackals in central Europe. These observations may reflect adaptability to diverse environmental factors, human influences, and hunting pressures. High population density combined with intensive hunting of jackals may lead to home range instability along with more frequent and long-distance dispersals, attributable to the disruption of the family structure and contributing to the rapid expansion of jackals across Europe. The rapid range expansion of jackals in Europe raises new legislative issues. Comprehending the mechanisms driving the change in jackal distribution is essential for determining research, management, and conservation priorities.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animal trapping and handling activities were conducted according to Hungarian legislation on hunting and with relevant authorization (permission number SO/FM/02856-1/2020).

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the first author upon reasonable request.

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