



## Research Article

## Temporal trends of home range sizes and movement patterns of peri-urban golden jackals in Belgrade, Serbia

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### Abstract

The golden jackal is currently expanding in Europe, but little is known about its movement ecology and space utilisation in these newly colonised areas. The species high adaptability to different diets and habitats, together with the absence of large predators are often considered the main drivers of its great success in recent decades. Immense human-caused habitat alteration is expected to further exacerbate this process. Understanding what factors drive changes in movement patterns and space use is of crucial importance for the establishment of adequate management policies. Here, we analysed temporal variations in the movement patterns and home range sizes of 14 jackals (7 males and 7 females) fitted with GPS collars from 2017 to 2022, in an area characterised by high human impact. Our results showed that movement patterns varied not only between sexes, but also between daytime periods and throughout the year. Both males and females moved significantly more during the night, with males traveling greater distances compared to females. In addition, jackals exhibited notable variations in movement patterns across the year, with movement rates possibly influenced by reproductive phases and other environmental factors such as food availability and cold weather. Jackals' home ranges were significantly influenced by sex, daytime period and time of year. In addition, night ranges were consistently larger than day ranges, for both males and females. These results provide insight into movement ecology of jackals in an area with high anthropogenic pressure and can serve as a basis for developing appropriate population management strategies.

## Introduction

The range of the European golden jackal (*Canis aureus moreoticus* Geoffroy, 1835) has been expanding towards the northwest in Europe, with a noticeable increase in recent decades. In 2021, its presence was reported in over 33 European countries (Hatlauf et al., 2021), and since then reproductive groups have been reported as far north as Estonia (Männil and Ranc, 2022), while individual jackals have been found in the Norwegian (Sørensen and Lindsø, 2021) and Russian subarctic (Rykov et al., 2022). In the west, a reproductive pair has been recorded in Germany (Böcker et al., 2022) and recently the jackal has been found in Spain (de Buruaga et al., 2023). Before its rapid expansion, the golden jackal had a limited distribution in south-eastern Europe, although the exact period of colonization remains controversial (Spassov and Acosta, 2019). What is certain is that its range is expanding so rapidly that it is considered the largest documented carnivore population expansion in Europe (Spassov and Acosta, 2019). The expansion can be partly attributed to the highly adaptable opportunistic omnivorous diet of the jackal (Penezić and Ćirović, 2015; Lange et al., 2021), the extermination of wolves (an important apex predator of jackals) (Krofel et al., 2017), climate change (Arnold et al., 2012; Pyšková et al., 2016), changes in land use (Šálek et al., 2014) and other human-caused environmental changes such as deforestation and road expansion (Spassov and Acosta, 2019).

Today, the golden jackal can be found throughout Serbia. The lowlands around the Danube, Sava and Morava rivers are characterized by particularly high jackal densities with an average of 1.1 groups/10 km<sup>2</sup> (Šálek et al., 2014). This area has been described as the core area

of jackal distribution in Serbia (Ćirović et al., 2008). From a genetic standpoint, Serbian jackal populations appear to be most closely related to other populations in the Pannonian Plain (Stronen et al., 2021), specifically Slavonia (Croatia), wherefrom they receive approximately 25 % immigrants per generation, although these values may be inflated according to Fabbri et al. (2014). The same study revealed a low level of historical and current gene flow between the Serbian (Serbia-Slavonia) jackals and those in Dalmatia (Croatia) and Bulgaria, indicating significant isolation from each other. This seems to be in accordance with Zachos et al. (2009), where no variation was found in the mtDNA sequences and nuclear variability was very low. Further findings by Stronen et al. (2021) confirmed the relative isolation of the Serbian (Pannonian) population of jackals from Dalmatia.

Radio-telemetry, and by extension GPS telemetry has been used to obtain some unique types of data on carnivores that are not possible or otherwise too challenging through other methods. Telemetry data is particularly useful for understanding animals' movement and space use, mapping dispersals and migrations, determining resource use and selection, population density, fecundity and mortality causes, as well as intraspecific and interspecific relationships (Boitani and Powell, 2012). As jackal expansion leads to increased encounters with humans in Europe, understanding aspects of their ecology, and in particular movement ecology in rural and semi-urban areas is crucial. To date, a modest number of telemetry studies on jackals have been published, mostly in Asia (Poché et al., 1987, Gitajatov, 1965 in Demeter and Spassov, 2005; Jaeger et al., 2001, Jaeger et al., 2007; Aiyadurai and Jhala, 2006; Patil and Jhala, 2008; Rotem et al., 2011; Jenks et al., 2015; Charaspet et al., 2019; Kamler et al., 2021; Katna et al., 2022) among which only a few were based on samples larger than a couple of individuals with extended tracking periods. In addition, only a handful of studies have been

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conducted in Europe (Giannatos, 2004; Lanszki et al., 2018; Fenton et al., 2021; Frangini et al., 2022; Csányi et al., 2023), where jackal expansion is particularly intense and a ubiquitous phenomenon. Small sample sizes have limited robust analyses, leaving our understanding of the biological and environmental factors influencing golden jackal movement patterns and home range sizes incomplete. Available evidence does indicate a clear temporal pattern, with jackals moving more during nocturnal periods than in the daytime (Jenks et al., 2015; Fenton et al., 2021). The influence of sex has been studied but without definitive conclusions (Fenton et al., 2021). Seasonal variations have also been investigated, though mostly within the tropical part of the jackals' range and with smaller sample sizes (Kamler et al., 2021;  $n = 3$ ). Notably, Katna et al. (2022) ( $n = 7$ ) examined both sex and seasonal (Cool-Dry, Hot-Dry, and Wet season) influences on home range size in India, finding no significant effects of these factors. In summary, our understanding of how these factors influence space use and movement in jackals remains inconclusive, and no research has yet explored how they may interact or vary in influence in relation to one another.

The increasing range of the golden jackal over human dominated landscapes in Europe and the suspected change in movement patterns in rural and peri-urban areas could become more relevant in the coming years. The role of jackals in domestic animal predation under certain conditions has been documented several times and may either occur occasionally (Giannatos, 2004) or it may occur more frequently and be exacerbated by the way humans deal with animal waste (Genov and Vassilev, 1991; Yom-Tov et al., 1995). Attacks on humans have also been recorded recently in Israel and it is suspected these attacks may have resulted from expanding populations feeding on discarded food and animal waste with the added risk of rabies potentially contributing to the aggression (Surkes, 2021). The jackal's habitat and diet driven predisposition for parasites have led to it being considered an important wild reservoir of human and animal parasites (Gherman and Mihalca, 2017). On the other hand, jackals have been described as important providers of ecosystem services through the consumption of animal waste and the control of rodent populations (Ćirović et al., 2016).

In this paper we describe temporal variations in the movement patterns and home range sizes of jackals living in peri-urban areas in Serbia. We present novel data on a larger than before reported GPS dataset collected on jackals living near Belgrade, Serbia. By utilizing more sophisticated methods not previously applied in the study of jackals, we attempted to elucidate important details of jackal ecology in this environment. In particular, we hypothesized that movement patterns and range sizes would differ between sexes, as well as throughout the year depending on the periods of the day.

## Methodology

### Study area

The jackals were monitored within Surčin, a peripheral municipality of Belgrade. The study area is part of the South Pannonian Plain, covers ~ 470 km<sup>2</sup> and contains 7 settlements with about forty-seven thousand inhabitants and a population density of 164 per km<sup>2</sup>. The area is intersected with several highways as it is an important interchange on the road through, from and to Belgrade. The climate is continental with average daily temperatures ranging from -20 in the winter up to 40°C in summer (Pavlović et al., 2017). The study area borders the Sava River in the south and is intersected by many irrigation canals, which are used by jackals as denning, resting or hiding places. Agricultural lands cover 72.7 % of the area, with wheat, sunflower, soybean and maize being the most dominant crops, while the rest of the study area is occupied by forests (11.3 %) and other miscellaneous terrain including built up infrastructure (16.4 %) (Municipal Assembly of Surčin, 2021). The study area contains numerous illegal dumps that sporadically emerge, where waste from meat processing and other types of organic waste are frequently discarded. Furthermore, leftovers of domestic animals (mainly pigs and chickens) are a common food source for jackals during winter and spring, when small mammals are not so abundant (Penezić and Ćirović, 2015). The golden jackal is a game species in Serbia and can be hunted all year round.

### Data collection

We captured jackals between 2017 and 2022 using Belisle 6"- foot snare traps (Wildlife Control Supplies, LLC). The only exception was a breeding pair (M1 and F1) caught with box traps. Jackals were chemically immobilized with an intramuscular injection of 100 mg tiletamine and zolazepam (Zoletil for injection, Virbac; initial vol 10 mg/kg). Standard body measurements were taken at each capture, and age was estimated based on the jackal's size, sexual maturity, period of capture and tooth wear inspection (Lombaard, 1971) (see Table 1. for summary information). As no specific protocols or licenses are required for non-laboratory work with jackals in Serbia, we adhered to standard protocols for work with protected mammals. These were specified under licences to conduct fieldwork as part of field teaching and research issued through contracts with the Ministry of Education, Science, and Technological Development (Licence no: 451-03-65/2024-03/2 00178; 451-03-66/2024-03/200178). Due to the high hunting pressure in the area, it was considered unlikely that any of the captured individuals were older than 3 years (ranging from yearlings (<1) up to 3 years). All jackals were collared with Vertex Lite GPS collars (GPS Plus; Vectronic Aerospace GmbH, Berlin, Germany) and a timer-controlled drop-off system and later released at the trap site. All GPS collars were scheduled to record a location every 3 hours (8 positions/day), with the exception of two individuals whose collars were initially set to a 4-hour fix interval and were corrected to a 3-hour interval shortly thereafter. The GPS relocation success rate ranged from 86–100 % (mean: 97 %; Tab. 1), except for one individual for which approximately 58 % of the data was missing. However, considering that gaps were relatively evenly distributed over time, we used the data in further analysis.

### Data preparation and analysis

We analysed movement patterns for 7 males (F1-F7) and 7 females (M1-M7) tracked over periods ranging from 20 days (F5) to 401 days (M6), resulting in a total of 24,558 locations (Tab. 1, Figure S1 in Supplementary). Out of 14 tracked individuals 3 were killed before drop-off activation (M1 and F5 were shot by hunters and F7 was run over by a vehicle). Each individual was grouped as either yearling (<1 year) or adult ( $\geq 1$  year) (Tab. 1).

All statistical analyses were conducted in the R statistical environment (version 4.2.2) (R Core Team, 2022) using packages made for it. We extracted sunrise and sunset times for each day for UTC time zone (Universal Time Coordinated) with the "suncalc" package (Thieurmél and Elmarhraoui, 2022). We defined daytime periods as the time period from sunrise until the sunset (day) and nighttime from sunset until sunrise (night). To better categorise the movements, we further defined day/night movement with the criteria that if jackal movement began within 1.5 h or less before sunrise/sunset, the derived tracks were considered as day/night.

The movement and home range analysis were conducted with the "move" (Kranstauber et al., 2023) and "adehabitatHR" packages (Calenge, 2006). As we were primarily interested in movement in or near their home ranges, we excluded fixes collected during three multiday forays for two of the male jackals which we deemed extensive enough to influence the later analysis. These multiday forays were delineated based on visual inspections of tracks and net squared displacement (NSD) values extracted using the "amt" package (Signer et al., 2019). This resulted in the removal of a total of 133 fixes, accounting for 399 hours of movement from the two jackals. The home ranges and core areas were calculated using 99 %, 95 % and 50 % utilisation distribution (UD) minimum convex polygon values (MCP) (Mohr, 1947), Kernel Density Estimator (KDE) (Worton, 1989) with the reference bandwidth ( $h_{ref}$ ) and the dynamic Brownian Bridge Movement Model (dBBMM) developed by Kranstauber et al. (2012). Since dBBMM was shown to be the most efficient compared to other methods (MCP, KDE) regarding type I (under smoothing) and type II (over smoothing) errors (Silva et al., 2018, 2020; Wilson et al., 2020) it was used for further monthly and daytime range analysis with a 95 % UD, while the MCP

Table 1 – Data used in the home range and movement analysis of peri-urban jackals in Serbia, 2017 - 2022. \* jackals with both 3h and 4h fixation intervals.

Jackal ID	Age category	Tracking start	Tracking end	No of days	No of fixations	Gps success rate
M1*	adult	12/3/2017	11/10/2017	214	1695	92.7
M2	adult	28/11/2019	18/5/2020	173	1362	99.2
M3	adult	6/12/2019	6/11/2020	337	2668	99.2
M4	adult	10/1/2020	13/12/2020	339	2673	98.9
M5	yearling	20/12/2020	26/3/2021	97	753	98.3
M6	adult	14/5/2021	18/6/2022	401	3194	99.7
M7	adult	12/12/2021	28/12/2022	382	3013	98.8
F1	adult	12/3/2017	17/7/2017	128	879	86.4
F2	adult	5/4/2019	20/9/2019	169	1340	100
F3*	adult	23/5/2019	23/4/2020	337	2668	99
F4	adult	19/6/2021	27/1/2022	223	1735	97.9
F5	yearling	9/10/2021	28/10/2021	20	155	100
F6	adult	6/11/2021	14/9/2022	313	2312	92.7
F7	yearling	8/2/2022	9/4/2022	61	201	41.8

and KDE were included along with dBBMM for total home range estimations for easier comparison with other studies.

dBBMM combines the Brownian bridge movement model (BBMM) (Horne et al., 2007) and the behavioural change point analysis (BCPA) to estimate the UD of an animal, based on its movement path and a varying Brownian motion variance ( $\sigma^2$  m) parameter that reflects changes in the movement behaviour along the trajectory (Kranstauber et al., 2012). The underlying assumption of temporal dependence for BBMM allowed us to incorporate both the tracks with different fixation intervals (3h and 4h) into the home range analysis as well as data with single fixation point loss resulting in 6h or 8h intervals.

For KDE, the size of the grid was set to 1000 and the grid extent to 2.5. The same grid values were used for dBBMM, while the window size was set to 9 and the margin to 3 following the instructions by Kranstauber et al. (2012). This helped capture a biologically relevant time frame (i.e., the differences in day-night movement patterns of the jackals) which we also kept when computing monthly ranges. When computing ranges for day and night, the window size was adjusted to 17 and margin to 7 in order to capture movement changes across longer periods. The GPS error was set to 15 m according to field tests. In cases when dBBMM failed to determine the home range or home range appeared circular due to uncertainty of position, the code was instructed to ignore gaps larger than 9h (Smola et al., 2023). We used the same method to ignore the gaps between nights or days when daytime ranges were computed.

To analyse jackals' movement patterns, we first constructed regular movement trajectories for every jackal and then extracted 3h movement distances as the Euclidean distance between two successive fixes. Then, we calculated median values for movement distances for each jackal in all months and daytime periods (day/night). 4h movement distances in case of M1 and F3 individuals were excluded from this analysis. In order to avoid sampling bias due to a non-balanced sample, we first calculated medians of movement distances for each individual, and further extracted means of those values for all predefined categories. Movement distances are presented in km/day, except in the case of daytime periods where they are shown in m/3h for better understanding and comparison.

To test for differences in movement patterns, we fitted a series of alternative linear mixed-effect models (LMM) with movement distances as the response variable and different combinations of explanatory variables (sex, age, time of day, month, hour, season) using the "lme4" package (Bates et al., 2014). Steps shorter than 15 m were excluded to reduce the influence of hardware error. The remaining steps were then log transformed, and a mean value was calculated per every day/night to more closely match the temporal resolution of our predictor variables. This resulted in a total of 5979 mean step lengths used. To control for repeated measures of individuals, all models were fitted with the jackal ID as a random effect.

The specification of the model was selected based on sequential testing of hierarchical modelling with the "anova" function from the "stats" package (?) including comparing AIC (Akaike Information Criteria) values and  $R^2$ , RMSE and Sigma values using the "performance" package (Lüdecke et al., 2021) (Table S2 in Supplementary). The final movement distance model included ID as a random effect and sex, month and daytime as fixed effects with a combination of crossed effects between them while the rest of the covariates were insignificant or correlated to other effects. The final model specification was:

$$\log\_dist \sim \text{sex} \cdot \text{daytime} + \text{month} \cdot \text{daytime} + \text{sex} \cdot \text{month} + (1|id).$$

To test for differences in range sizes we used the same approach as with step lengths and fitted a set of alternative LMM models with log transformed dBBMM areas and sex, daytime, and month as explanatory variables. Our input variable was range size in  $\text{km}^2$  calculated from all days or nights for every month with a set minimum of 20 unique dates of telemetry data (days/nights). This yielded a total of 197 range values. We evaluated the range model in the same way as the step length model (Table S3 in Supplementary) and settled for a LMM with log transformed areas and the following specification:

$$\log\_area \sim \text{daytime} + \text{sex} \cdot \text{month} + (1|id).$$

Significance was calculated using Satterthwaite's method to estimate degrees of freedom and generate p-values using the "lmerTest" package (Kuznetsova et al., 2015). In order to make predictions when not all combinations of factors were significant, model-based bootstraps ( $n=1000$ ) were implemented using the "bootMer" command from "lme4" to obtain confidence intervals. Values were back-transformed to  $\text{m}/3\text{h}$  and  $\text{km}^2$ , respectively, for better model interpretation. Both models were assessed using the "DHARMA" (Hartig, 2022) and "performance" (Lüdecke et al., 2021) packages. Data visualisation was done using the "ggplot2" package (Wickham, 2016).

## Results

### Movement distances

The overall 3-hour movement distances (steps) varied between 0 km, representing the resting state up to 7.2 km. During their forays a maximum distance of 11.4 km was recorded for individuals M3 and M7. The median movement distance was 1.99 km/day ( $SE=0.2$  km/day), with males traveling longer daily distances (median =  $2.31 \pm 0.32$  km) compared to females (median =  $1.68 \pm 0.2$  km) (Table S1 in Supplementary).

Differences in movement patterns were observed between the periods of the day, with jackals moving less during the day (median 3h movement distance =  $70.3 \pm 7.7$  m) compared to the night (median 3h movement distance =  $602.8 \pm 80.9$  m). In addition, differences in movement patterns were also registered between the sex categories. Males moved slightly less than females during the day

Table 2 – Type III Analysis of Variance Table of fixed effects for the movement distance model with Satterthwaite’s method.

	Sum of Squares	Mean Square	Numerator Degrees of Freedom	Denominator Degrees of Freedom	F value	Pr(> F)
sex	3.24	3.24	1	11	4.2594	0.06355
daytime	1793.33	1793.33	1	5946.1	2354.08	0.001 ***
month	68.62	6.24	11	5793	8.1893	0.001 ***
sex × daytime	16.39	16.39	1	5946.9	21.513	0.001 ***
daytime × month	148.01	13.46	11	5942.3	17.6625	0.001 ***
sex × month	73.19	6.65	11	5792.1	8.7337	0.001 ***

(69.2 ± 11.7m/3h and 71.5 ± 11.7m/3h, respectively), while the opposite pattern was observed during the night (747.8 ± 130.4m/3h and 457.8 ± 65.8m/3h for males and females, respectively) (Table S4 in Supplementary).

Daily movement distances varied across months, with the lowest values registered in November (median daily distance = 1.71 ± 0.33km) and the highest value in July (median daily distance = 3.19 ± 0.67km). A summary of the monthly movement statistics can be found in the Supplementary (Table S5 in Supplementary).

The best performing model showed that step lengths were significantly affected by time of day and month and their interactions with sex (R<sup>2</sup> = 0.39, Tab. 2). The analysis of random effects (ID) yielded an Intraclass Correlation Coefficient (ICC) of 0.10. A summary of the model can be found in the Supplementary (Table S6 in Supplementary).

The model results showed that the jackal movement was most influenced by time of day (F=2354.08, p < 0.001). When fitted as an individual factor, sex had marginally significant influence on jackal movement (F=4.25, p=0.06), but showed more significant effects when interacting with time of day (F=21.51, p < 0.001) and months (F=8.73, p < 0.001). According to our model predictions, jackals moved significantly more during the night compared to daytime hours throughout the year (Fig. 1, Table S7 in Supplementary). In general, males travelled longer distances than females (Fig. 1) for most of the year, but no significant difference was detected overall (β = 0.194, t = 1.1, p = 0.28; see Table S6 in Supplementary). The only exceptions were September (both for day and night) and October and November (only during the day), when females moved more.

Furthermore, the movement patterns of the two sexes differed over the course of the year (Fig. 1, Table S7 in Supplementary). During the night, males started to increase their movement in January reaching a peak in March (~950 m/3h), followed by a relatively steady decrease until the end of the year. Contrary to the males, females maintained similar movement rates during the spring and summer, after which they showed an increase, reaching a peak in September (~550 m/3h, Fig. 1, Tab. S7). During the day, the differences in movement patterns between the sexes were less pronounced. Our results suggest contrasting patterns during the winter months, with movement increasing in both sexes during the day and decreasing at night (Fig. 1).

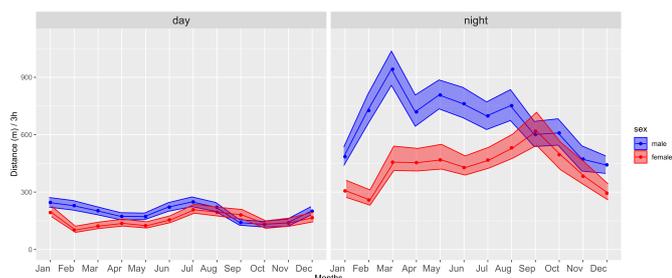


Figure 1 – Prediction graph of jackal movements based on sex, month and daytime in Serbia, 2017-2022. Ribbon widths represent 90% confidence intervals.

### Home ranges

Our results showed a large variability in 95 % dBMM home ranges, both between sexes and between individuals of the same sex. Males had twice as large average home ranges compared to females (17.07 ± 4.91 km<sup>2</sup> and 7.56 ± 1.83 km<sup>2</sup>, respectively; Tab. 3). For males, home ranges varied from 2.82 km<sup>2</sup> to 43.09 km<sup>2</sup> while for females, they ranged from 0.79 km<sup>2</sup> to 12.17 km<sup>2</sup>.

Daytime range variations showed a clear pattern, with the average night range being almost three times larger compared to day range (13.86 ± 3.34 km<sup>2</sup> and 4.63 ± 0.98 km<sup>2</sup>, respectively). Furthermore, the same pattern was found within sex categories (for males: 19.91 ± 5.57 km<sup>2</sup> and 7.82 ± 1.46 km<sup>2</sup> on average for night and day, respectively, and 6.52 ± 2.27 km<sup>2</sup> and 2.74 ± 0.91 km<sup>2</sup>, for females, respectively). For males, night ranges ranged from 3.21 km<sup>2</sup> up to 47.44 km<sup>2</sup>, while during the day they ranged from 1.38 km<sup>2</sup> to 12.64 km<sup>2</sup>. For females, the largest values for night and day ranges were 19.06 km<sup>2</sup> and 6.79 km<sup>2</sup>, while the smallest were 1.1 km<sup>2</sup> and 0.15 km<sup>2</sup> respectively. A summary of the diel ranges can be found in the Supplementary (Table S8).

The best performing model showed that jackal range sizes were significantly influenced by sex, periods of the day and month (R<sup>2</sup>=0.66; see Tab. 4.). The analysis of random effects (ID) yielded an Intraclass Correlation Coefficient (ICC) of 0.25.

Variations in jackal monthly ranges were most affected by time of day (F = 219.29, p < 0.001). A summary of all effects can be found in the Supplementary (Table S9). The reference of the model represented a female jackal’s range in April during the day (β<sub>0</sub> = -0.75, t = -19.8, p = 0.05). In general, night ranges were significantly larger than day ranges (β = 1.82, t = 14.8, p < 0.001; Fig. 2, Table S10 in Supplementary). Males had larger range sizes than females with a marginally significant effect (β = 0.94, t = .92, p = 0.059). The only exceptions were August (both day and night) and September (night), when females increased their range area sizes compared to males (β = 1.24, t = 2.82, p < 0.01; Fig. 2).

### Discussion

Although the range of jackals has extended considerably in recent periods, there are still only a limited number of studies on the jackal home range sizes and movement capabilities. Most of these studies have been conducted in regions where jackals have historically been present longer, in South and Southeast Asia (Poché et al., 1987; Jaeger et al., 2001, 2007; Aiyadurai and Jhala, 2006; Patil and Jhala, 2008; Jenks et al., 2015; Charaspet et al., 2019; Kamler et al., 2021; Katna et al., 2022), and West Asia (Gitajarov, 1965 in Demeter and Spassov, 2005; Rotem et al., 2011). In recent years an increasing number of telemetry studies on golden jackals have been conducted also in Europe (Gianatos, 2004 (n of jackals = 5); Lanszki et al., 2018 (n=1) Fenton et al., 2021 (n=6); Frangini et al., 2022 (n=8); Csányi et al., 2023 (n=3)). However, the discussion and comparison of values becomes challenging considering the differences in methodology and sampling intervals in accordance with the authors’ means and objectives in their respective studies.

Obtained results confirmed that jackal movement patterns and home ranges are highly influenced by time of the day and further vary throughout the year and between sexes.

Table 3 – Summary values of home ranges at 95% and 99% UD and core areas at 50% UD for individual jackals, using MCP,  $K_{\text{href}}$  and dBBMM.

ID	MCP95	$K_{\text{href}}$ 95	DBBMM50	DBBMM 95	DBBMM 99
F1	8.2	10.7	0.77	8.83	13.91
F2	28.1	37.0	0.77	12.01	25.27
F3	3.7	3.0	0.21	3.52	8.92
F4	2.4	1.8	0.33	2.17	4.81
F5	0.4	0.8	0.09	0.79	1.74
F6	18.4	16.0	0.73	12.17	38.39
F7	11.0	18.1	0.62	10.45	17.39
M1	13.0	13.7	1.29	11.50	18.49
M2	92.3	79.0	2.52	43.07	76.96
M3	37.9	39.6	1.11	15.91	34.72
M4	17.3	11.9	1.12	11.52	21.67
M5	14.3	18.1	1.46	10.28	23.49
M6	2.7	3.0	0.45	2.82	4.84
M7	41.0	27.7	1.77	22.04	38.96
Average	20.8	20.0	0.9	11.9	23.5
Average female	10.3	12.5	0.5	7.1	15.8
Average male	31.2	27.6	1.4	16.7	31.3

### Movement distances

Our results showed that the average step lengths of jackals in our study area were consistent with the results obtained in other studies (Lanszki et al., 2018; Charaspet et al., 2019; Fenton et al., 2021), despite the different fixation schedule (6h (resampled), 4h and 6h (resampled), respectively). Jackals showed higher movement rates during the night compared to the day and the same pattern was observed in both males and females. The nocturnal activity of jackals has also been shown in other studies as well (Rotem et al., 2011; Jenks et al., 2015; Fenton et al., 2021) and most likely represents a strategy to avoid encounters with humans that are more active during the day, and may be additionally corroborated by the heavy hunting pressure that occurs in the daytime. Similar patterns have been observed across a range of mammalian species (Gaynor et al., 2018). In addition, males showed significantly higher movement rates during the night compared to females. This could be related to the dispersal behaviour of males which has been registered in the study area (Potočnik et al., 2022). However, given that females in our study area mostly had home ranges closer to human settlements, it could be assumed that the proximity to anthropogenic food sources may lead to lower movement rates in females.

Furthermore, our model prediction showed pronounced variation in jackal movement patterns throughout the year (Fig. 1). In particular, in late autumn and early winter (until January), both males and females decreased their movements during the night, while their movements increased during the day. The observed pattern is probably related to the gradual decrease in environmental temperature, which causes jackals to shift their movement to daytime hours when movement may be less energy demanding. A similar pattern has been observed in other mammalian species, such as white-tailed deer (*Odocoileus virginianus*) (Beier and McCullough, 1990) and some mice and vole species (*Peromyscus leucopus* and *Myodes gapperi*; *Mus musculus*) (van der Vinne et al., 2014; Guiden and Orrock, 2020). In addition, previous research on jackal diet in Serbia has shown that jackals maintain optimal body condition during the winter months (Penezić et al., 2022), probably as a result of an energy-rich diet dominated by domestic animal leftovers (Penezić and Čirović, 2015), which presum-

ably spoil more slowly in cold weather. The period also coincides with pig slaughtering activities so more slaughter waste may be available. Therefore, further research is needed to evaluate whether and to what extent abundant and easily accessible anthropogenic food resources of that type might influence the movement behaviour of jackals in peri-urban areas.

Jackals exhibited an opposite pattern from January until late autumn, with movement during the night being more pronounced than movement during the day. The first movement peak occurred in March, when the average daily movement distance was  $2.79 \pm 0.45$  km (Table S5 in Supplementary). Although there are insufficient data on the jackal mating season (according to field observations and interviews with hunters, it occurs from February to early March), our results suggest that the observed movement patterns are most likely influenced by mating behaviour. Similar observations have also been shown for other canid species such as foxes (Saunders et al., 1993; Cavallini, 1996; Mueller et al., 2018) and coyotes (Andelt, 1985; Sasmal et al., 2019). Another possible reason for the observed pattern could be related to the increased presence of rodents in the jackals' diet (Penezić and Čirović, 2015), which jackals may need to seek out more actively. Interestingly, the increase in overall movement is more pronounced in males than in females. This discrepancy might suggest that males exhibit greater movement rates as they search for unpaired, receptive females. The difference increases towards the end of the mating season, as fewer females might still be eligible for mating and therefore more effort is required for males. Both males and females decreased their movement during the day in May, followed by a gradual increase towards summer, reaching a peak in July. Contrastingly, females showed no significant fluctuations in nocturnal movement during this period, while males exhibited more pronounced variations, with their movement rate decreasing significantly in April and July. We suspect that the April–May shift is related to the birth of pups after which males maintain a higher movement rate, presumably because they forage for the whole pack and then gradually reduce movement as the offspring mature and require less parental care. The lower movement rate observed in females is prob-

Table 4 – Type III Analysis of Variance Table of fixed effects for the distance model with Satterthwaite's method.

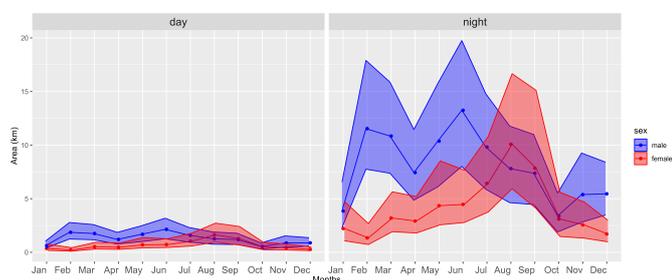
	Sum of Squares	Mean Square	Numerator Degrees of Freedom	Denominator Degrees of Freedom	F value	Pr (>F)
month	24.89	2.26	11	189.41	3.07	<0.001***
sex	4.21	4.21	1	14.118	5.72	0.031*
daytime	161.54	161.54	1	185.55	219.3	<0.001***
month × sex	15.8	1.44	11	189.41	1.95	0.036*

ably related to pup rearing. As the new generation becomes self-reliant, the differences between males and females become less pronounced.

From July to September females showed a contrasting movement pattern significantly narrowing the gap in nightly movement and even moving more than the males during both day and night in September (Tables S6 and S7 in Supplementary). This could simply be due to females returning to the *status quo* as they invest less time into rearing the pups. Alternatively, the jackals' body condition may be the deciding factor. In their research, Penezić et al. (2022) showed that females had lower Kidney Fat Index (KFI) values than males in summer and autumn, suggesting poorer body condition due to the large energy investment into pup rearing. Therefore, we assume that the higher movement rates observed in females during this period may be related to the increased foraging to improve their body condition. These assumptions are consistent with findings that showed females were in significantly better body condition than males later in winter (Penezić et al., 2022).

## Home ranges

The average night ranges were approximately three times larger compared to average day ranges. This is consistent with previous findings of Rotem et al. (2011), who showed that jackals had significantly smaller day ranges regardless of the distance from settlements. Males showed larger average home ranges than females. However, only a marginally significant ( $p=0.059$ ) influence of sex as a standalone factor was found in our range model, possibly due to the smaller sample size and larger variability compared to the movement model. There was no significant interaction between sex and time of day but some differences appeared based on the month. In coyotes, an ecologically similar and taxonomically related species, varying results have been found; males having larger home ranges (Riley et al., 2003), females having larger home ranges (Holzman et al., 1992; Chamberlain et al., 2000) or no difference between the sexes (Grinder and Krausman, 2001, Gosselink, 1999 in Gosselink et al., 2003; Gehrt et al., 2009; Franckowiak et al., 2019). Most researches on the topic tend to agree with the review findings of Laundré and Keller (1984) that there is no difference in home range size based solely on sex in coyotes. A similar lack of pattern has been observed in foxes (Henry et al., 2005; Drygala and Zoller, 2013; Walton et al., 2017), where home range size is most likely also, not sex dependant (Henry et al., 2005). Considering the lack of strong evidence in our range model, lack of consistent similar differences in coyotes and foxes and the fact that individual jackal pairs have been found to have a similar sized home range (Fenton et al., 2021; Kamler et al., 2021; Csányi et al., 2023) we find it unlikely that jackals have a home range size difference that is strictly sex based. However, sex differences on a seasonal basis may exist depending on the individual's reproductive status as evidenced by our model predictions (Fig. 2).



**Figure 2** – Prediction graph of jackal monthly range sizes based on sex, month and daytime in Serbia, 2017-2022. Ribbon widths represent 90% confidence intervals.

In our study, there was a large share of individuals with a home range smaller than 5 km<sup>2</sup> ( $n=4$ ), with most falling between 10 to 15 km<sup>2</sup> range. Smaller home ranges than 5 km<sup>2</sup> have been reported (Poché et al., 1987; Jaeger et al., 2001), but never over such a long period of time. These smaller home ranges are probably related to anthropogenic food sources, which are often found near settlements. This is consistent with Rotem et al. (2011), who found a significant effect of settlements on home range and core area sizes (i.e., jackals tended to reduce their

home ranges when close to settlements). Our longest tracked jackal (401 days) had an exceptionally small home range (2.82 km<sup>2</sup>), separated from a settlement by only a small canal, and with fixes recorded ~70 m from the nearest street. It can be assumed that jackals exposed to abundant anthropogenic food sources do not need to forage as often as it would be expected in more natural areas, resulting in smaller home ranges. Previous studies have shown that other canid species such as foxes and coyotes exhibit a similar pattern along the natural-urban habitat gradient (reduced home range sizes and increased population density) (Atwood et al., 2004; Bino et al., 2010; Šálek et al., 2015).

Due to insufficient data regarding the breeding status of the tracked individuals, we were unable to evaluate the influence of this variable on jackal movement patterns. In addition, hunting pressure in the study area is high throughout the year, causing many social structures to be disturbed, possibly changing jackal behaviour. Further research is therefore needed on how breeding status, as well as hunting pressure, affects jackal movement patterns.

## Conclusion

The jackal's opportunistic diet, often based on discarded food and animal waste, is expected to favour the species' expansion in urban and peri-urban areas, where such waste is more abundant. As jackals increasingly adapt to these new surroundings, further conflicts may arise from population expansion, particularly considering their proclivity for hosting parasites and predation on domestic animals under certain conditions. Therefore, understanding the jackal's movement ecology in rural and semi-urban areas is not only important for fundamental research on the species ecology, but also provides essential information for the development of appropriate management strategies.

Our results revealed that jackals' movement patterns in rural and peri-urban areas were significantly influenced by the time of day, and varied across different periods of the year and between sexes. These movement patterns might also be shaped by jackals' reproductive status, along with the presence of anthropogenic food sources and high hunting pressure. As a result, our findings can serve as a basis for further research to help distinguish the various factors influencing jackal space use and help quantify the influence of human influences. These insights can inform the introduction of targeted population management policies at local and regional scales, such as adjusting hunting pressure during specific times and periods of the year to optimize resource allocation. 🐾

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## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

**Table S1** Summary of step lengths by individual.

**Table S2** Model comparison for different nested models of log-transformed movement distance.

**Table S3** Model comparison for different nested models of log-transformed range sizes.

**Table S4** Summary of diel movements.

**Table S5** Summary of median daily movements by month and sex.

**Table S6** Summary of effects for the movement model.

**Table S7** Predicted values of distance travelled per Linear mixed model.

**Table S8** Summary of day and night home ranges per individuals.

**Table S9** Summary of effects for the home range areas model.

**Table S10** Predicted values of home range area size per Linear mixed model.

**Figure S1** Map of study area with jackal fixes captured between 2017-2022.