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Movement, space-use and resource preferences of European golden jackals in human-dominated landscapes: insights from a telemetry study

Skye Fenton[1,2] · Paul R. Moorcroft[1] · Duško Ćirović[3] · József Lanszki[4] · Miklós Heltai[5] · Francesca Cagnacci[1,2] · Stewart Breck[6,7] · Neda Bogdanović[3] · Ilija Pantelić[3] · Kornél Ács[4] · Nathan Ranc[1,2,8]

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Abstract

During the last half-century, the distribution of golden jackals (*Canis aureus*) has rapidly increased throughout Europe. Today, golden jackals are thriving in human-dominated landscapes across Southeastern and Central Europe. Most studies on golden jackals have focused on large-scale distribution patterns; to date, little is known about the species' fine-scale spatial ecology. In this study, we analyzed the movement behavior, space-use and resource selection of six golden jackals fitted with GPS-GSM collars in two study areas in Hungary and Serbia. Two of the jackals were a breeding pair. We found that home range size averaged 11.2 km^2 (90% autocorrelated kernel density estimation), and was characterized by significant individual-level variability (range 1.3–32.5 km^2). Golden jackal movements and resource selection were strongly influenced by circadian patterns: during the day, jackals travelled an average of 300 m every 6 h, and all monitored individuals selected for vegetation cover, often near edges. At night, golden jackals travelled significantly further (1 km 6 h^{-1}), and were more likely to venture outside of cover into agricultural areas. Movement analysis of the breeding pair revealed that the male and female tended to remain in close proximity during the day, but ranged more independently at night. Altogether, our findings suggest that golden jackals' ability to thrive in human-dominated landscapes rely on a fine spatio-temporal avoidance of humans.

Keywords *Canis aureus* · Bio-logging · Fragmentation · Mesocarnivore · Proximity analyses · Step selection analysis

Introduction

Historically restricted to small areas along the Mediterranean and Black Sea coasts, European golden jackals (*Canis aureus moreoticus* Geoffroy Saint-Hilaire, 1835) have undergone a considerable range expansion over the last 50 years

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✉ Nathan Ranc
nathan.ranc@gmail.com

[1] Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

[2] Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, 38010 San Michele All'Adige, Italy

[3] Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia

[4] Carnivore Ecology Research Group, Szent István University, Kaposvár Campus, 40 Guba Sándor Str, 7400 Kaposvár, Hungary

[5] Department of Wildlife Biology, Institute for Conservation of Natural Resources, Szent István University, Gödöllő Campus, Páter Károly str. 1, 2100 Gödöllő, Hungary

[6] USDA-National Wildlife Research Center, 4101 LaPorte Ave, Fort Collins, CO, USA

[7] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Colorado, USA

[8] Environmental Studies Department, University of California Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA

(Arnold et al. 2012; Trouwborst et al. 2015). The species is now well-established throughout Southeastern Europe (Ranc et al. 2018), and is currently expanding into northern and western European countries. Reproductions have been reported as far as the Czech Republic (Jirku et al. 2018) and northern Poland (Kowalczyk et al. 2020), and a small population has formed in Estonia (Rutkowski et al. 2015; Männil and Mustasaar 2018; Ranc et al. 2018). Furthermore, dispersers are being noted as far as Denmark, France (Andru et al. 2018) and the Netherlands (Eijkelkamp 2020). It has been hypothesized that the expansion of this generalist mesocarnivore has been facilitated by the historic persecution of the grey wolf (*Canis lupus*) (Krofel et al. 2017), the availability of anthropogenic food, and land use changes (Lanszki et al. 2018a). Over the last decade, the species' expansion has triggered increasing public, stakeholder, and policy-maker interest (Trouwborst et al. 2015). However, the study of golden jackals in Europe is still in its infancy, and important knowledge gaps in the species' natural history and ecology have hindered the development of evidence-based management.

Similar to the current expansion of the coyote (*Canis latrans*) and the crab-eating fox (*Cerdocyon thous*) in the Americas (Hody et al. 2019), European golden jackals are expanding into human-dominated environments. At the population level, previous studies have shown that jackals in the Balkan Peninsula exhibit a high plasticity in selected habitats (Šálek et al. 2014a; Spassov and Acosta-Pankov 2019), reaching the highest densities in heterogeneous farmlands and wetlands. In addition, genetic evidences (Rutkowski et al. 2015) and telemetry studies (Lanszki et al. 2018b) have shown that golden jackals are able to successfully disperse over large distances in human-dominated landscapes. Beyond population-level analyses (Giannatos et al. 2005; Krofel 2007; Šálek et al. 2014a) or dispersals (Lanszki et al. 2018b), we still lack understanding of the fine-scale spatial behavior of resident golden jackals in Europe. In human-dominated landscapes, mesocarnivores can reduce the risk of encounters with humans by modulating their movements and habitat selection spatio-temporally (Carricondo-Sanchez et al. 2019). For example, coyotes avoid daytime interactions with humans through use of vegetative cover and tend to be much more active at night in anthropogenic landscapes (Grinder and Krausman 2001; Way et al. 2004; Mitchell et al. 2015; Santana and Armstrong 2017). In Europe, highly adaptable red fox (*Vulpes vulpes*) are predominantly nocturnal, and typically rest in cover during the day (Lucherini et al. 1995).

In this study, we aim to characterize the spatial ecology of European golden jackals in human-dominated landscapes (agricultural lands interspersed with woodlands and urban areas, characterizing large portions of Central and Southeastern Europe). We analyzed the movement patterns, space-use and habitat selection of six individuals fitted with GPS-telemetry collars in two separate study areas in Hungary and Serbia. Our overarching hypothesis is that golden jackal movement behavior is driven by spatio-temporal avoidance of human activity. First, we assessed the circadian patterns in golden jackal movements, and predicted that jackals move significantly more at night than during daytime (P1) (Lanszki et al., 2018b). Second, we used a step selection analysis (SSA) (Fortin et al. 2005) to evaluate golden jackal habitat selection in response to distance to edge of cover and distance to buildings. We predicted that, during the day, golden jackals should select for areas within or near vegetation cover (P2), and avoid areas near buildings (P3). In addition, we provide the first telemetry-based estimates of home range size for golden jackals in Europe and the first account of the species sociality by analyzing the proximity between trajectories of a breeding pair in Serbia.

Methods

Study area

This study was conducted in two separate areas: southwest Hungary (Somogy county), and Northern Serbia (suburban area of Belgrade). In Hungary, the study area is characterized by a high forest cover (53.5%; primarily of English oak *Quercus robur*) interspersed with agricultural fields, and small settlements (Lanszki et al. 2018a, b). In Serbia, the study area is dominated by agricultural and open fields (85%), with most of the vegetative cover as forests fragments (primary English oak *Quercus robur*, European hornbeam *Carpinus betulus*), hedgerows and lush vegetation bordering water channels (primary *Salix* sp and *Populus* sp). In both study areas, golden jackals are the largest carnivores. In Hungary, golden jackals primarily consume small mammals in agricultural areas (Lanszki et al. 2006), and carrion or viscera of wild ungulates in forested areas, where high ungulates densities are managed for hunting (Lanszki et al. 2018a). In Serbia, the jackal's diet is generally dominated by domestic ungulates and poultry (as carcass leftovers) and small mammals, but can also include plants (mainly seeds, fruits, and grass), particularly in the summer and autumn (Penezić and Ćirović 2015).

Data collection

Movement data were collected for six golden jackals: two females in Hungary (HF1 and HF2), a male and female breeding pair in Serbia (SM1 and SF1), and two additional young females in Serbia (SF2 and SF3). The six golden jackals were between 10 months and 2 years of age upon capture and in good health (see Table 1 for individual information).

Table 1 Summary table for the six golden jackals monitored

Animal	Study area	Sex	Age (month)	Weight (kg)	Capture date	Last relocation date	Days monitored
HF1	Hungary	F	18	10.1	Oct 21, 2013	June 16, 2014	239
HF2	Hungary	F	10	9.5	Feb 24, 2015	Jan 25, 2016	336
SM1	Serbia	M	24	11.6	March 12, 2017	Oct 11, 2017	214
SF1	Serbia	F	24	9.1	March 12, 2017	July 17, 2017	128
SF2	Serbia	F	10	7.6	April 6, 2019	Sept 20, 2019	168
SF3	Serbia	F	12	8.4	May 23, 2019	Nov 30, 2019	192

All six animals were captured using baited box traps ($n = 4$) or Belisle 6″ traps ($n = 2$; SF2 and SF3), immobilized (see Supplementary Materials: Table A1 for details), and fitted with GPS telemetry collars able to record location data on pre-determined schedules. They were monitored for up to 11 months between 2013 and 2019. GPS relocations were collected every six hours in Hungary and every three hours in Serbia (data for SM1 and SF3 were initially taken every four hours, but the interval was changed to a 3-h schedule 2 months after collaring for SM1 and 2 days after collaring for SF3).

Data preparation

To enable direct comparison among all monitored golden jackals, we regularized the GPS telemetry data to homogeneous six-hour interval trajectories for the movement and space-use analyses (Calenge 2006). For the proximity analysis of the Serbian breeding pair, however, we used the native three-hour interval data. The Hungarian (HF2 and HF1) and Serbian (SF2 and SF3) animals' data were taken at 6:00, 12:00, 18:00 and 00:00 UTC; the data for the Serbian male–female pair, SM1 and SF1, was offset by 1 h (i.e., 5:00, 11:00, 17:00 and 23:00 UTC). GPS relocations were classified as either daytime (12:00 and 18:00 UTC; 11:00 and 17:00 UTC), or nighttime (00:00 and 06:00 UTC; 23:00 and 05:00 UTC). The total proportion of missing locations was overall low (except for HF1 during the denning period; Lanszki et al. 2018b). We did not interpolate missing data.

One golden jackal, HF1, dispersed from her natal home range over 12 days and 220 km (Lanszki et al. 2018b). Following Lanszki et al. (2018b), we used the MigrO clustering algorithm (Damiani et al. 2015, 2016) to delineate the dispersal transience (i.e., movements between natal and breeding home ranges). Because the dispersal movements of HF1 were significantly different from resident movements (e.g., higher speed) (Lanszki et al. 2018b), we excluded the dispersal transience (and an earlier dispersal attempt) from the analyses. We computed separate pre- (i.e., natal) and post-dispersal (i.e., breeding) home ranges. The trajectories of all individuals are shown in Fig. 1.

Movement and space-use analyses

To investigate golden jackal movement behavior, we computed the Euclidean distances between successive relocations (hereafter referred to as step length), and plotted the individual empirical distributions of step lengths for day and night, separately.

We then investigated golden jackal space-use using two complementary methods for calculating home range size. We calculated the 95% Minimum Convex Polygon (MCP) (Mohr 1947) as a reference value that allowed comparison with published literature. Because MCP tends to overestimate home ranges and has been shown to be biased by sample size (Seaman et al. 1999), we also calculated utilization distributions (Worton 1989) using autocorrelated kernel density estimates (AKDE) (Fleming et al. 2015b) in order to account for the autocorrelation between sucessive relocations. We then extracted the area (in square kilometers) corresponding to each animal's core area (50% contour) (Ranc et al. 2020) and home range (90% and 95% contours).

Resource selection analysis

To evaluate diel habitat selection in human-dominated landscapes, we conducted individual-level step selection analyses (SSA) (Fortin et al. 2005; Thurfjell et al. 2014) using geographic layers of vegetation cover and human buildings as covariates in interaction with time of day.

We obtained vegetation cover layers from two sources. For both study areas, we reclassified the 2015 tree cover density product from Copernicus pan-European, high-resolution layers (20-m resolution) (European Environmental Agency 2015) into high cover (≥ 45%) and low cover (< 45%; these thresholds were determined via a sensitivity analysis). For Serbia, we also considered water channels as cover, where reeds and riparian vegetation provide shelter to jackals (Ćirović et al. 2018); water channels were instead absent in our Hungarian study area. These were mapped through digitization of satellite images. We calculated the distance to cover ($\text{Dist}_{\text{cover}}$) as the Euclidean distance (in meters) to the nearest edge of vegetation cover: the value of zero denotes the edge itself, while negative values indicate

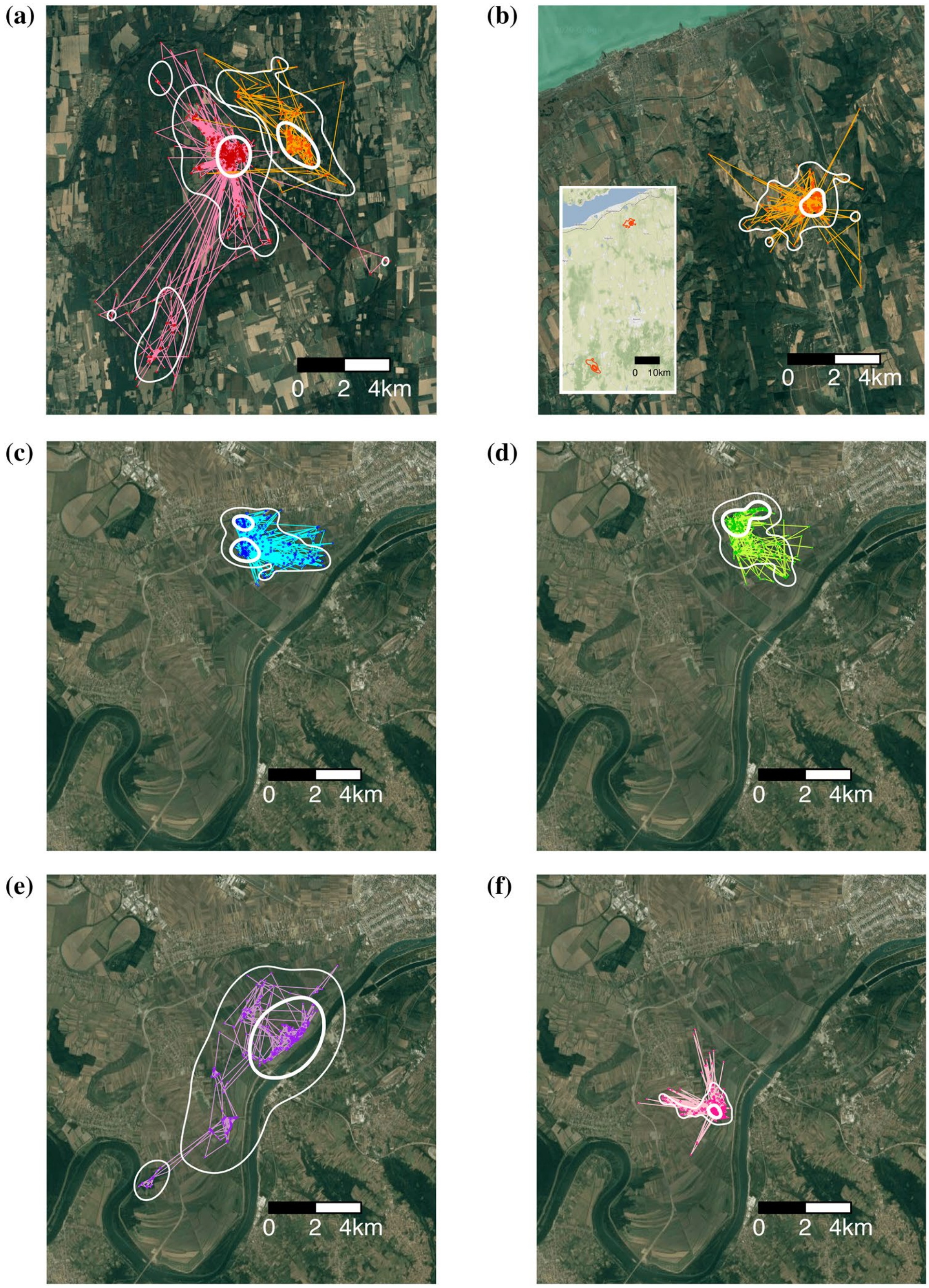


Fig. 1 Movement trajectories (colored lines and points), core area (50% autocorrelated kernel density estimate, AKDE, utilization distribution; thick white contour) and home range (95% AKDE utilization distribution; thin white contour) of all six golden jackals. **a** HF1 pre-dispersal (orange) and HF2 (red); **b** HF1 post-dispersal and insert displaying the distance between HF1's home ranges; **c** SM1; **d** SF1; **e** SF2; **f** SF3

distances within cover and positive distances indicate locations outside of cover. We included a second-degree polynomial for $\text{Dist}_{\text{cover}}$ as jackals may select for edge environments (i.e., low preference for areas deep within vegetation or far from vegetation cover, and peak at the vegetation edge, i.e., $\text{Dist}_{\text{cover}} = 0$) (Šálek et al. 2014a). We calculated the distance to the nearest building ($\text{Dist}_{\text{buildings}}$) as the Euclidean distance (in meters) to the nearest building, as mapped by the 2017 Copernicus European Settlement Map (European Environmental Agency 2017). We used satellite images and expert knowledge to remove abandoned structures and mis-classified objects from the base layer. In our study areas, buildings are primarily housing and agricultural constructions. We characterized the circadian patterns in jackal habitat selection through an interaction between the distance variables and a day/night covariate (Day).

For each GPS relocation, we generated twenty available locations by randomly sampling from the empirical step length distribution of each individual jackal, and using a circular uniform distribution to generate random directions for each available location (Thurfjell et al. 2014). We analyzed the data using a matched-control conditional logistic regression (Thurfjell et al. 2014), and used Akaike Information Criteria (AIC) (Burnham and Anderson 2002) for model selection. We determined a suitable core model for all animals (i.e., a unique set of variables across individuals) including a second-degree polynomial for $\mathrm{Dist}_{\mathrm{cover}}$ in interaction with Day, and $\mathrm{Dist}_{\mathrm{buildings}}$ in interaction with Day.

Proximity analysis

To gain insight into the sociality of the mated pair of jackals, we examined the relative proximity of the Serbian male and female, SM1 and SF1 through time. To do this, we calculated the Euclidean distance between animals for each simultaneous 3-h relocations between May 9th and July 17th, 2017. We then evaluated whether the observed distances differed from what would be expected by chance (i.e., the two individuals move independently of each other) through a permutation test (random shuffling of relocation pairs: 10,000 permutations). We then investigated whether the proximity between both individuals differed spatially across their home range and temporally (day versus night).

Softwares

We used the R (R Core Team 2016) packages adehabitatLT (Calenge 2006) and ctmm (Fleming et al. 2015a) for movement and space-use analyses respectively, the 'raster' package (Hijmans 2020) to calculate the distance layers for the SSA, and the survival package (Therneau 2020) for the conditional logistics (SSA). We used QGIS (QGIS Development Team 2016) and the 'Serval' plugin (Pasiok 2019) for manually cleaning and elaborating base maps.

Results

Movement patterns

Golden jackals travelled on average 662.5 m (95% CI 635.1–693.9) over six hours (temporal interval between successive relocations). Individual mean step length varied almost twofold (Table 2; Supplementary Materials: Fig. A1): from 438.7 m (95% CI 397.4–483.2) for the Serbian female SF2 to 849.7 m (95% CI 774.5–923.1) for the Serbian male SM1. Golden jackals travelled significantly longer distances at night (mean = 1009.1 m) than during the day (mean = 307.7 m; Mann–Whitney U test: $W = 966{,}698$, p value = < 0.001; Table 2; Fig. 2), supporting our first prediction (P1). The circadian pattern in distance travelled was particularly striking for the Serbian male SM1, for which night step lengths averaged 1523 m (95% CI 1426–1622), over nine times longer than the daytime average of 165.4 m (95% CI 139.0–198.8). For the remaining animals, the nighttime mean distances were 2.0 to 3.2 times greater than the daytime mean distances.

Space-use patterns

Golden jackal home ranges averaged 11.17 km^2 (90% autocorrelated kernel density estimate; AKDE), but with high inter-individual variation: from 1.33 km^2 for SF3 to 32.54 km^2 for SF2 (Table 2). Home ranges estimated using 95% Minimum Convex Polygon (MCP) were even more variable, ranging between 2.34 km^2 for SF3 and 66.57 km^2 for HF2 (Table 2). Core areas (50% AKDE) were much smaller: all were under 3 km^2 except for SF2, which was 8.55 km^2 (Table 2).

Resource selection

Golden jackals' selection for vegetation cover varied considerably between nighttime and daytime. During daytime, all individuals were most likely to be found within or close to high cover (as shown by the peak in relative probability of presence for negative distances to cover, i.e., within cover; see green lines in Fig. 3; Supplementary Materials: Table A2). By contrast, the monitored jackals were more likely to be in areas of low cover at night (as shown by the higher probability of presence for positive distances to cover at night as compared to daytime, purple and green lines in Fig. 3, respectively), supporting our second prediction (P2). In addition, nighttime selection patterns were more variable among individuals: HF1 and HF2 used areas relatively independently of vegetation cover during the nighttime (purple lines Fig. 3, panels a and b) while SF1 and SF2 displayed night-time preferences similar to those of daytime, staying relatively close to cover (purple lines Fig. 3, panels d and e). These differences in selection for vegetation between day and night translated into spatio-temporal patterns of resource use (Fig. 4; see abrupt variations in relative probability of presence during the day, panels e and f, in response to spatial variations in cover, panels c and d, as opposed to more homogeneous patterns of presence during the night, panels g and h). Looking at an example from each study area, HF2 and SM1 are not likely to be present in areas far from cover during the daytime, especially apparent given the narrow channel cover of SM1′s habitat (Fig. 4, panels e and f). At night, both animals are more likely to be present in areas further from vegetation cover (Fig. 4, panels g and h).

The influence of the distance to the nearest building, and its interaction with time of day, was less consistent among the monitored golden jackals (Supplementary Materials: Fig. A2). During the day, all animals except for HF1 selected for increasing distances from buildings, mostly supporting our third prediction (P3). However, during the night, three jackals (HF2, SM1 and SF3) selected for increasing distances

Table 2 Step length, core area and home range sizes for all six golden jackals

Animal	Mean step length (m)			AKDE area (km^2)			MCP area (km^2)
	Overall	Day	Night	50%	90%	95%	95%
HF1	762.4 (687.4–863.0)	473.0 (393.6–564.6)	1065.1 (952–1249)	2.16 (pre) 0.89 (post)	10.34 (pre) 5.48 (post)	15.26 (pre) 9.08 (post)	14.55 (pre) 9.88 (post)
HF2	776.8 (707.9–861.1)	366.8 (309.5–449.0)	1184.8 (1071–1312)	1.97	15.08	28.49	66.57
SM1	849.7 (774.5–923.1)	165.4 (139.0–198.8)	1523.0 (1426–1622)	1.29	6.75	8.94	8.39
SF1	564.5 (503.9–633.7)	253.3 (198.7–329.4)	808.7 (724.9–901.7)	1.68	6.71	8.76	6.45
SF2	438.6 (397.4–483.2)	279.0 (241.2–328.1)	590.4 (519.7–671.5)	8.55	32.54	42.06	19.47
SF3	499.9 (456.2–553.4)	248.6 (215.6–287.0)	751.2 (670.1–830.1)	0.21	1.33	2.39	2.34
Average	662.5 (635.1–693.9)	307.7 (283.9–336.1)	1009.1 (964–1063)	2.39	11.17	15.26	18.24

Step length means (95% confidence intervals in parentheses) are shown for the complete trajectories (overall), as well as separately for day and night. Core area size (in km^2) is calculated using the autocorrelated kernel density estimate (AKDE; 50% contour). Home range size is calculated using the 90% and 95% AKDE contours as well as the 95% Minimum Convex Polygon method (MCP)

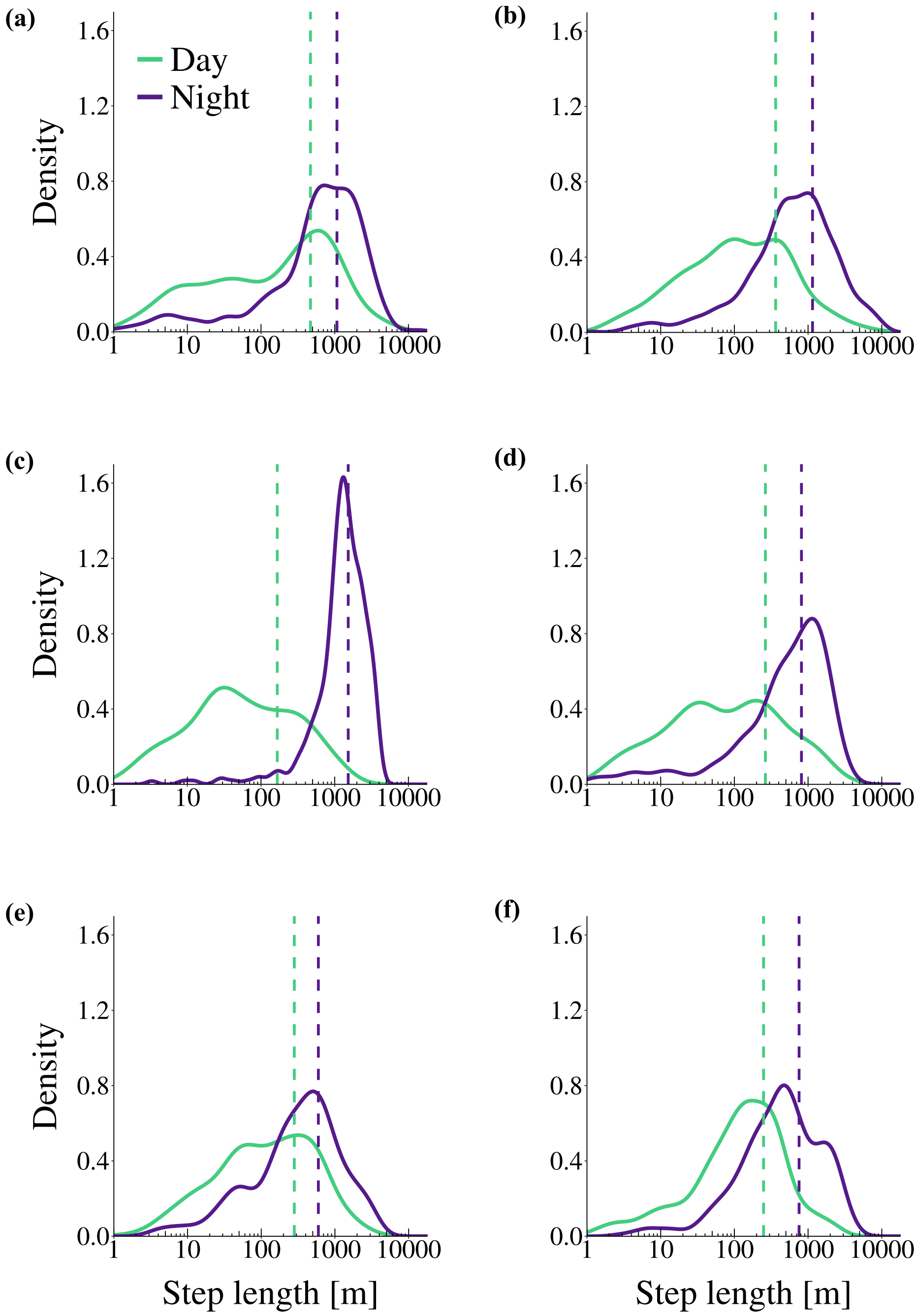


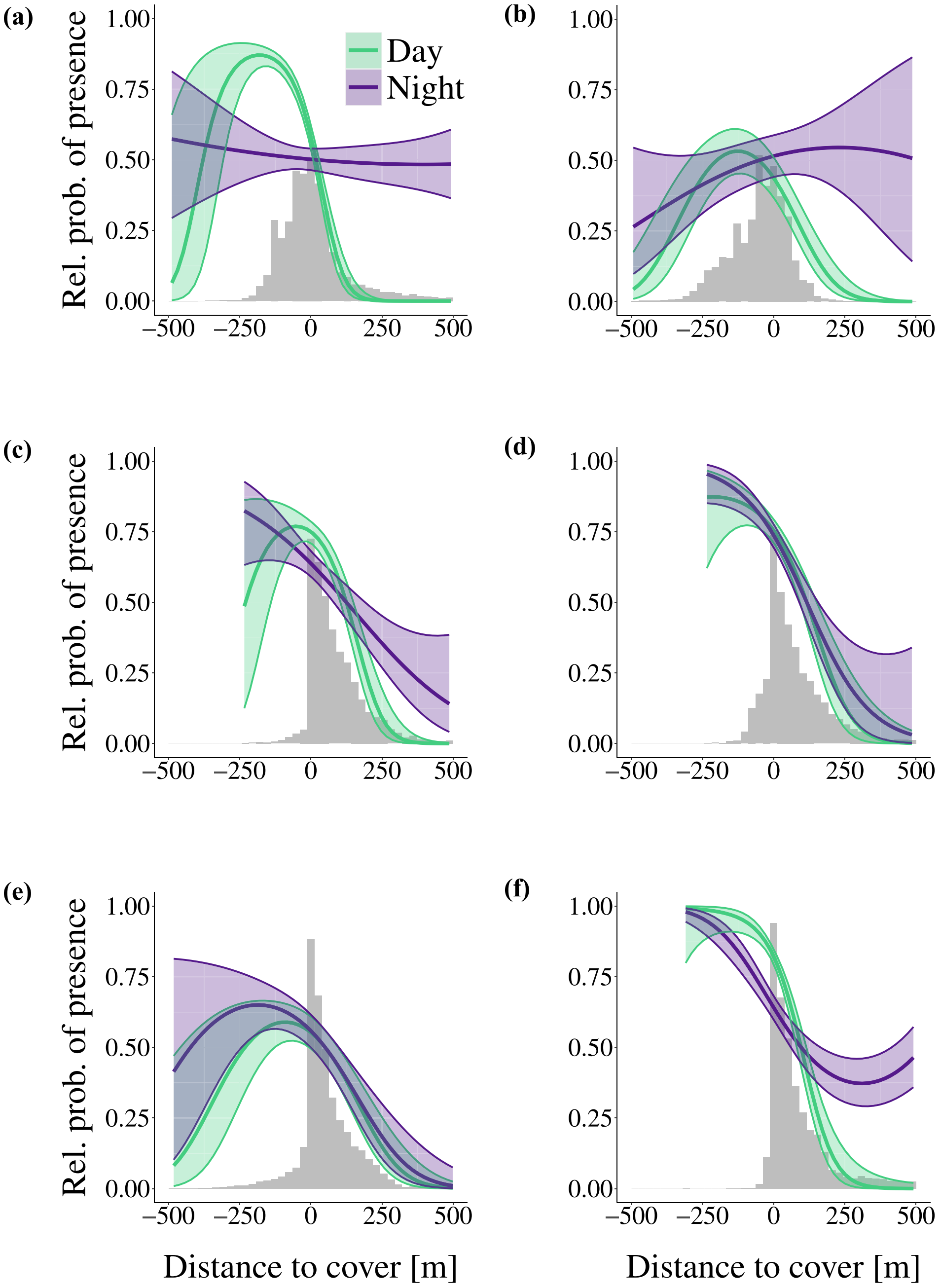
Fig. 2 Step length distributions (6-hour steps; in meters) for all six golden jackals plotted separately for day (green) and night (purple), on a log scale for visual clarity. The means of each group are shown with a dashed vertical line. Panels: **a** HF1; **b** HF2; **c** SM1; **d** SF1; **e** SF2; **f** SF3

from buildings, two animals exhibited no particular selection (SF1 and SF2), and one individual selected for decreasing distances from buildings (HF1). These nocturnal results showed less support for our third prediction (P3) but also highlight interesting differences in behavior between daytime and nighttime.

Proximity analysis

The golden jackal breeding pair (SM1 and SF1) generally stayed in close proximity. The distance between the pair was significantly larger at night (mean = 312.8 m) than during the day (mean = 184.1 m; Mann–Whitney *U* test: W = 35,103, *p* value < 0.001). On average, the actual distance between both individuals was significantly less than expected from chance (10,000 random permutations between paired relocations, *p* < 0.001; see Supplementary Materials: Table A3 and Fig. A3 for more details). The degree of proximity between the breeding pair did not exhibit any clear spatial patterns (see the absence of spatial clustering between location pairs closer than expected by chance; Supplementary Materials: Fig. A4).

Fig. 3 Golden jackal selection for distance to cover is mediated by circadian patterns. For each individual, the partial response plot shows the effect of distance to cover on the relative probability of presence for day (green) and night (purple). The available distribution of distance to cover is shown as a grey histogram. For the Serbian individuals (**c**–**f**), we truncated the response curves to not predict beyond the range of our data. **a** HF1; **b** HF2; **c** SM1; **d** SF1; **e** SF2; **f** SF3



Discussion

Here we show for the first time golden jackal's fine-scale movement behavior, space-use, and resource selection that allows the species to thrive in human-dominated landscapes, with potential implications for the understanding of the species range expansion across Europe (Arnold et al. 2012; Trouwborst et al. 2015; Krofel et al. 2017). In particular, golden jackals' circadian patterns of movement and resource preferences suggest they are able to thrive in human-dominated environments by modulating their behavior both spatially and temporally to avoid humans.

Our findings reveal the small-scale movement patterns of individual jackals. All of the animals had longer average steps lengths at night (Table 2), indicating that golden jackals are most active at night (P1). This is consistent with previous studies on radio-tracked individuals outside Europe (Rotem et al. 2011; Jenks et al. 2015). Coyotes studied in peri-urban environments in Arizona (Grinder and Krausman 2001) as well as suburban New England (Way et al. 2004) displayed similar nocturnal tendencies, suggesting

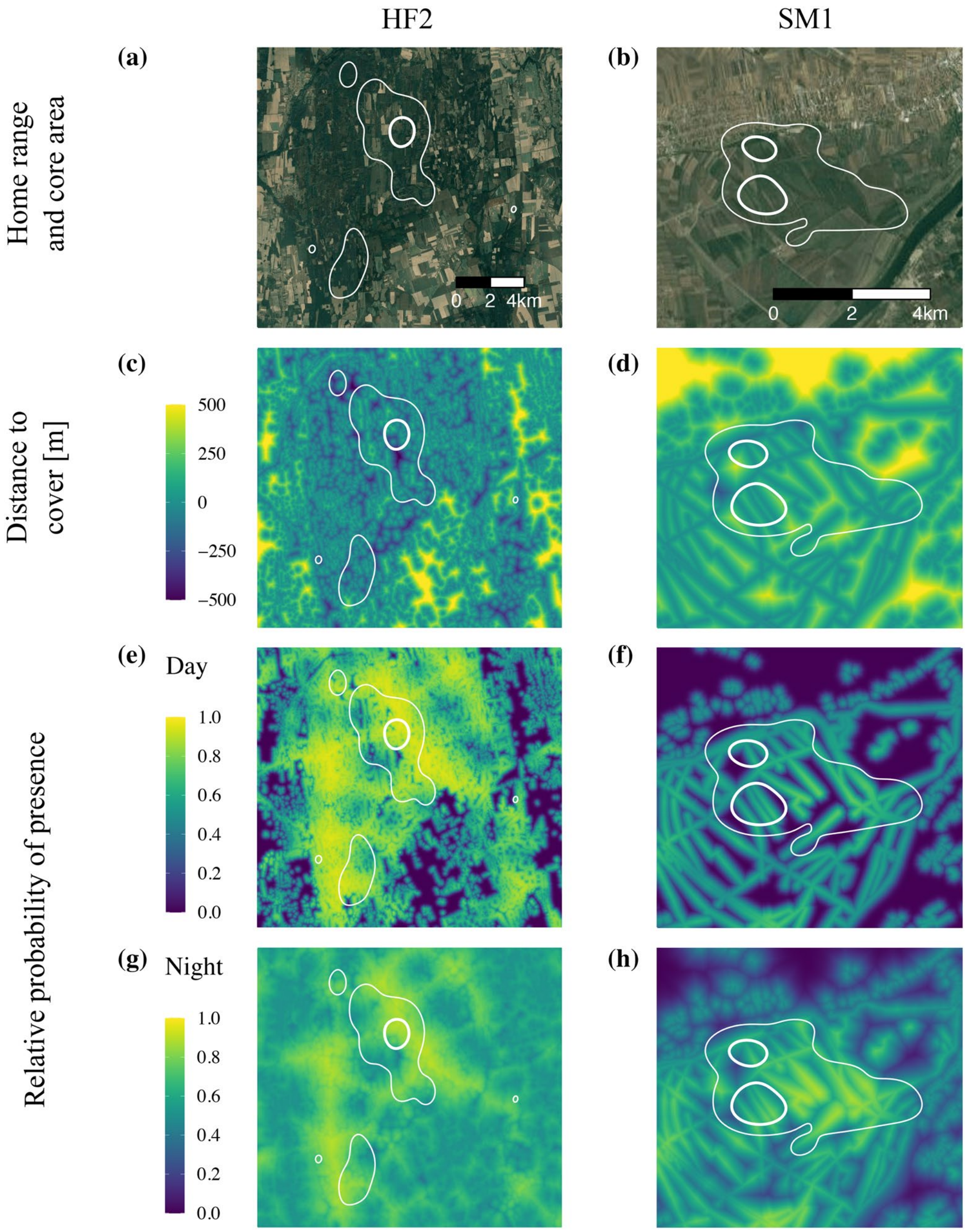


Fig. 4 Selection for cover varies with time of day. **a**, **b** The core areas (50% autocorrelated kernel density estimate, AKDE, utilization distribution; thick white contour) with home ranges (95% AKDE utilization distribution; thin white contour) for two golden jackals—HF2 (in Hungary; **a**) and SM1 (in Serbia; **b**)—over an aerial photograph background. **c**, **d** The distance to nearest vegetation cover (in meters), primarily woodlands patches for HF2 (blue/dark green areas on **c**), and water channels for SM1 (blue/dark green linear features on **d**). **e**–**h** The relative probability of presence, as predicted by the step selection analysis, during the day (**e**, **f**) and night (**g**, **h**). During the day, jackals are more likely to be within cover (yellow/green areas on panels **e** and **f** correspond to low distance to cover, areas in blue/dark green on **c** and **d**, respectively). At night, jackals are more likely to use areas further away from cover as shown by the more homogeneous probability of presence across the landscape (see lower contrast between low and high cover probability of presence on **g** and **h** as compared to **e** and **f**)

that the ability of mesocarnivores to avoid humans is key to their success in human-dominated landscapes. Our results show important individual variability in golden jackal movement behavior. Although all females displayed an increase of nighttime step length of 2–3 times over their daytime steps (Table 1), the two females in Hungary had average step lengths 1.5–2 times longer than the females in Serbia. This difference may be explained by the fact that the more forested landscape in the Hungary study area provides more cover for movement (Šálek et al. 2014a), or that foraging resources tend to be more distant. Interestingly, the monitored male (SM1) averaged the longest night-time steps, 9 times longer than his daytime average steps (Table 2). Our sample size does not allow us to make definitive conclusions on sex-differences; such variability in spatial behavior have been observed in other mesocarnivores, e.g. in coyotes when females are tending pups (Way et al. 2004) but not generally in jackals (Moehlman 1987).

Many estimates have been published regarding jackal population densities in various parts of Europe (Giannatos et al. 2005; Krofel 2007; Šálek et al. 2014a), but GPS-based estimates of home range size have been lacking. We found the average home range size for the six golden jackals in our study to be 11.2 km^2 (90% AKDE) with a much smaller average core area size of 2.4 km^2 (50% AKDE). In Greece, home range size for three individuals fitted with VHF collars varied from 2.2 to 15 km^2 (Giannatos 2004). Previous studies conducted in Thailand (Charaspet et al., 2019), Israel (Rotem et al. 2011), India (Aiyadurai and Jhala 2006), and Ethiopia (Admasu et al. 2004) also yielded home range estimates consistent with our findings. Although there is high inter-individual variation in home range size estimates (range 1.3–32.5 km^2 90% AKDE), the intra-individual estimates across methods (AKDE and MCP) show a consistent pattern (Table 2). This suggests the individual variability reflects influential ecological factors rather than the methodology used to calculate home range sizes. The study of coyotes in inter-urban Arizona found a similarly large range of sizes among individuals' home ranges (Grinder and Krausman 2001). Human development is likely contributing to the observed variability; for example, home range size tends to be smaller near or within human settlements in many mesocarnivores (Šálek et al. 2014b). In Israel, jackals living far from settlements occupy larger home ranges and undertake longer foraging movements than individuals located near villages, where anthropogenic resources are abundant (Rotem et al. 2011). In our case, it is likely that an important food source prompted HF2's longer, more frequent forays to the southwest (Fig. 1, panel a) and consequently larger home range size.

Previous fine-scale studies of jackals indicated an ability to adapt to relatively intense farmland with significant open fields in Africa (Admasu et al. 2004) and in the Balkan Peninsula, though observed only in population-level studies (Šálek et al. 2014a). Here, our findings indicate that golden jackals remain within or near dense vegetation cover during the day, when human activity peaks (Fig. 3; P2). This is consistent with previous findings that jackals—as well as other mesocarnivores, e.g., coyotes (Mitchell et al. 2015), red fox (Hradsky et al. 2017)—prefer cover edges and small patches of vegetation over either large open spaces or heavily forested areas (Červinka et al. 2011; Šálek et al. 2014a). During the night, golden jackals were more likely to venture out of cover (Fig. 4), perhaps to find better foraging opportunities in the vicinity of settlements (Ćirović et al. 2016), and on agricultural land; diet analyses (Lanszki et al. 2006) found that jackals prefer voles (*Microtus* sp.) living in open fields over bank vole (*Myodes glareolus*) inhabiting forests. Our results are further consistent with findings that Indian golden jackals prefer areas of high cover during the day while venturing out to the periphery of villages at night (Aiyadurai and Jhala 2006). Altogether, these results suggest that fine spatio-temporal use of cover is key to the ability of golden jackals to adapt to human-dominated landscapes.

Overall, golden jackals selected for areas further away from buildings when humans are most active, during the day (Figure A2 in supplementary materials; P3). In contrast to the effects of vegetation cover, however, jackal selection for the distance to buildings exhibited a high degree inter-individual variability. In particular, one individual (HF1) appeared to select for areas closer to human buildings than expected by chance. In this study, we grouped all human constructions into a single category (i.e., buildings). However, buildings may be associated with different human activities (e.g., residential versus agricultural and livestock husbandry or even abandoned constructions), and consequently be more or less repulsive/attractive to jackals. Such heterogeneity in the ecological influence of buildings likely contributed to the observed inter-individual variability and illustrates the adaptability of these animals. For example, red fox individuals living in more human-dominated regions have been known to select for urban areas in response to the local availability of anthropogenic food sources (Alexandre et al. 2020). The selection for the distance to buildings in mesocarnivores is likely mediated by the presence of nearby cover; coyotes that have become successful residents in the suburban–rural interface in the US use vegetation cover that is within 50 m of buildings, even during the day (Way et al. 2004; Mitchell et al. 2015).

Our study also investigated the social interactions of European golden jackals. We found that the monitored breeding pair was in closer proximity than expected by chance, suggesting a close cooperative living between mated pairs, with the male and female foraging together. This is consistent with observations that mated jackal pairs in Africa hunt, rear young, and defend their territory together (Moehlman 1987). SF1 and SM1 tended to be farther apart at night, possibly because the male ventured farther on nighttime foraging expeditions. Additional months of observation could shed light on the seasonal variations in jackal sociality.

This study provides the first insights into the fine-scale spatial ecology of golden jackals in Europe and shows that jackals are able to coexist with humans and limit interactions by modulating their spatio-temporal behavior. Unlike coyotes in North America (Newsome et al. 2015), golden jackals have not yet colonized European urban centers—a niche currently occupied by red fox (Tolhurst et al. 2020).

Given the species adaptability and plasticity, European cities may soon become golden jackal's new frontier.

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Code availability The analyses relied on established statistical procedures described in the reference literature.

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest/competing interests.

Ethics approval The capture and tagging of wild golden jackals followed the official wildlife research procedures of Hungary and Serbia, respectively.

Consent for publication All the authors give their consent for publication.

Availability of data and material Golden jackals are heavily hunted in the study areas. Consequently, in the interest of wildlife conservation, we regret that the detailed locations will not be made publicly available.

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