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Research article

Seasonal activity patterns and home range sizes of wolves in the human-dominated landscape of northeast Türkiye

J. David Blount[1], Austin M. Green[2], Mark Chynoweth[3], Kyle D. Kittelberger[1], Dário Hipólito[4,5], Katarzyna Bojarska[6,7], Emrah Çoban[8], Josip Kusak[5] and Çağan H. Şekercioğlu[1,8,9]

[1]University of Utah, Salt Lake City, UT, USA
[2]Science Research Initiative, University of Utah, Salt Lake City, UT, USA
[3]Department of Wildland Resources, Utah State University – Uintah Basin, Vernal, UT, USA
[4]CESAM and Departmento of Biology, University of Aveiro, Campus Universitário de Santiago, Aveiro, Portugal
[5]Veterinary Biology Unit, Faculty of Veterinary Medicine, University of Zagreb, Zagreb, Croatia
[6]Wildlife Sciences, Faculty of Forest Sciences and Forest Ecology, University of Goettingen, Göttingen, Germany
[7]Centre of Biodiversity and Sustainable Land Use, University of Goettingen, Göttingen, Germany
[8]KuzeyDoğa Society, Türkiye
[9]Department of Molecular Biology and Genetics, Koç University, Istanbul, Türkiye

Correspondence: Judson David Blount (blount060@gmail.com)

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Gray wolves *Canis lupus* comprise one of the most widely distributed carnivore species on the planet, but they face myriad environmental and anthropogenic pressures. Previous research suggests that wolves adjust their time- and space-use seasonally to mitigate risks from humans, conspecifics, and other predators while maximizing their hunting and reproductive success. With many populations of wolves resettling in areas with dense human populations, understanding how wolves may adjust their temporal and spatial patterns in these more human-dominated landscapes is of high conservation importance. Typically, human presence causes wolves to increase their nocturnality and home range size. Here, we look at how seasonal home range size and diel activity patterns among resident and non-resident wolves differ in an ecosystem that experiences significant differences in human activity between seasons. While non-resident wolves had larger home ranges than resident wolves, there were no differences in home range sizes within residents and non-residents between seasons, suggesting that seasonal changes in human presence had no effect on home range size. The activity patterns of wolves were similar between seasons, but resident wolves had greater overlap with humans and were more active than non-resident wolves when humans were less present in the landscape. Both resident and non-resident wolves showed increased nocturnality, with both groups selecting for nocturnality more strongly in the nomadic season. This is the first study of tracking Türkiye's wolves and offers the first descriptions of the temporal and spatial trends of GPS-collared wolves in this highly human-dominated environment.

Keywords: anthropogenic pressure, camera trap, GPS tracking, spatial behavior

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Introduction

Few orders of terrestrial mammals can exert top-down control over an ecosystem like the members of Carnivora (Beschta and Ripple 2009, Estes et al. 2011, Ripple et al. 2014, Su et al. 2022). Gray wolves *Canis lupus* (hereafter 'wolf') provide some of the best-studied (Brooke et al. 2014) and wide-ranging examples (Wolf and Ripple 2017) of the effects carnivores can have in an ecosystem. Wolves potentially mediate cascading effects on their ecosystems through top-down control of meso-predators (Paine 1969, Soulé et al. 1988, Prugh et al. 2009), disease regulation (Pacala and Roughgarden 1984, Crooks and Soulé 1999, Ostfeld and Holt 2004, Ripple et al. 2014, O'Bryan et al. 2020), and influencing the spatial and temporal trends in home range size, habitat use, and activity of prey by inducing a landscape of fear (Fortin et al. 2005, Stoks et al. 2005, Trussell et al. 2006, Creel and Christianson 2008). However, many of these processes, combined with livestock predation, often place wolves in direct competition with people, increasing the likelihood of human–wildlife conflict (Ripple et al. 2014, Braczkowski et al. 2023). To mitigate this potential conflict, wolves often modify their own spatial habitat use and temporal activity patterns (Theuerkauf et al. 2003, Kusak et al. 2005, Roffler et al. 2018, Haswell et al. 2020, Kautz et al. 2021, Smith et al. 2022).

Adapting to human presence has defined the success or downfall of wolf populations across the globe (Chapron et al. 2014, Ausband and Mech 2023). The success of wolves can be, in part, credited to their ability to adapt through their generalist nature and dietary plasticity (Mladenoff et al. 1995, Mech and Boitani 2003, Griffin et al. 2023). However, these adaptations can affect fitness to varying degrees. Fluctuations in diel activity may change how carnivores interact with their prey (Patten et al. 2019), conspecifics, or competitors (Di Bitetti et al. 2010, Haswell et al. 2020). Changes in home range size can alter their chance of encountering risk in the form of humans or competitors (Ripple et al. 2014). Furthermore, if home ranges shift, the quantity and quality of available resources within each individual's home range will also change. Alterations in home range size and daily activity patterns have been shown to happen in response to short-term differences in human activity (e.g. the weekend effect: Nix et al. 2018, Suraci et al. 2021, Green et al. 2023) as well as in long-term trends (e.g. increased nocturnality: Theuerkauf et al. 2003, Kusak et al. 2005).

There are many external factors that have been shown to shape a wolf's long-term temporal and spatial patterns, including top-down and bottom-up effects. The abundance of prey (Wydeven et al. 1995, Mech and Boitani 2003, Jedrzejewski et al. 2007), habitat quality (Kittle et al. 2015), and the density of conspecifics (Peterson et al. 1984, Ballard et al. 1987) are negatively correlated with home range size, while latitude (Okarma et al. 1998, Mattisson et al. 2013, Petroelje et al. 2019) and density of certain anthropogenic features (i.e. roads and settlements; Rich et al. 2012, Mancinelli et al. 2018) are positively correlated. Traditionally, wolves are thought to have a crepuscular, bimodal activity pattern that mirrors the behavior of their main prey, ungulates (Curio 1976, Mech and Boitani 2003, Theuerkauf 2009). However, wolves that frequently encounter humans or use anthropogenic food sources have been shown to regularly increase their nocturnality (Kusak et al. 2005, Theuerkauf 2009, Newsome et al. 2013, Petroelje et al. 2019).

The degree to which anthropogenic factors affect wolf home range sizes and activity patterns has only recently garnered scientific attention and is highly context-specific (Theuerkauf 2009, Muhly et al. 2019, Dennehy et al. 2021). As wolves recolonize large, human-dominated parts of Europe and the USA (Chapron et al. 2014, Fabbri et al. 2014, Kuijper et al. 2016, Ditmer et al. 2022), understanding how wolves may adapt to anthropogenic influences can help guide wolf management. While temporal and spatial trends of wolves' activity and space use are generally understood in intact ecosystems with low human population densities (Jedrzejewski et al. 2007, Boyce 2018, Mclaren and Patterson 2021, Griffin et al. 2023), studies in highly human-dominated environments are scarce and mostly based on limited data (i.e. 1–2 wolf packs; Mancinelli et al. 2018). Therefore, understanding these trends for wolves in more anthropogenically disturbed systems is critically needed (Kuijper et al. 2016, Mancinelli et al. 2018, Haswell et al. 2020, Parsons et al. 2022).

To understand the effect anthropogenic and environmental factors may have on wolves, we must first examine a wolf's life cycle and how nutritional demands may change across seasons. The life history of wolves can be simplified into two seasons: pup-rearing and nomadic (Mech and Boitani 2003). Pup-rearing begins in spring with the birth of pups (Mech 2002, Schmidt et al. 2008, Roffler and Gregovich 2018). Since wolves are cooperative breeders, the rest of the pack modify their movements into a centripetal pattern, and reduce their daily ranges and activity levels (Theuerkauf et al. 2003, Eggermann et al. 2009, Vicedo et al. 2023) and regularly return to the den or rendezvous sites (Jedrzejewski et al. 2001, 2007, Walton et al. 2001) to provide support and protection for the pups. This pup-rearing season lasts into the late summer when pups begin to join the adults away from the den and rendezvous sites. During the nomadic season, wolves revert to pack-based hunting strategies to increase their hunting success in winter (Benson and Patterson 2015, Nordli et al. 2023).

Primarily during the fall to early winter, before the breeding season begins, young and sexually mature wolves may leave the pack and disperse to either find a mate or claim their own territory (Mech and Boitani 2003, Jimenez et al. 2017). Whereas resident wolves usually move within stable home ranges, these single individuals do not show any pronounced site fidelity (Fuller et al. 2003) and use larger areas (Mancinelli et al. 2018). This period of solitude means that wolves are much more likely to die from hunger, disease, people, or other wolves (Person and Russell 2009, Jimenez et al. 2017). It has been shown that dispersing wolves differ from resident wolves in that they are less likely to avoid human structures (Mancinelli et al. 2019), have more diurnal

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activity patterns, and generally are active for more of their day (Kirilyuk et al. 2021).

In this study, we used 12 years of data gathered from 31 GPS-collared wolves and five years of data collected from a camera trapping array in a human-dominated ecosystem in northeastern Türkiye to document the home range size and temporal activity trends of pack-based (hereafter, 'resident') and solitary (hereafter, 'non-resident') wolves in the pup-rearing and nomadic seasons. Specifically, we assessed how core and total home range sizes vary between and among resident and non-resident wolves during their pup-rearing season and nomadic season. Furthermore, we quantified the differences in activity patterns and the proportion of the day spent active between resident and non-resident wolves across seasons. Finally, we compared how anthropogenic activity and temporal trends may drive wolf spatial and temporal patterns. As human presence varies significantly across seasons within our study area, we hypothesized that resident wolf spatio-temporal behavior will also adapt to this variation in human presence. However, as non-resident wolves are not subject to the same nutritional demands and behavioral modifications of cooperative pup-rearing, they will not have seasonal variations in their spatio-temporal behavior. We predicted that: 1) resident wolves will increase their nocturnality, decrease their activity levels, and have smaller home range sizes during the season of intense human presence (pup-rearing season); 2) when human presence is lower (nomadic season), resident wolves will become less nocturnal, will have higher activity levels, and will increase their home range size; 3) activity overlap between wolves and humans would decrease in the pup-rearing season when human abundance is higher; and 4) non-resident wolves will have larger home ranges, increased nocturnality, and higher overall activity levels than resident wolves, but should not show differences between seasons.

The terms 'home range' and 'territory' are considered to be the same, since territory is the defended home range (Mech and Boitani 2003). However, this paper looks at individual space use for a single season and does not consider pack dynamics nor direct or indirect territorial defense mechanisms. Therefore, the authors have decided to use the term 'home range' in place of 'territory' (Goszczyński 1986, Okarma et al. 1998). Furthermore, as non-resident wolves do not defend territories, it would be inappropriate to describe the areas they use as 'territories' (Jedrzejewski et al. 2007). This use of 'home range' instead of 'territory' has been regularly accepted in the literature (Ciucci et al. 1997, Okarma et al. 1998, Kusak et al. 2005, Jedrzejewski et al. 2007, Mattisson et al. 2013, Mancinelli et al. 2018, Roffler et al. 2023).

Material and methods

Study site

This study is part of a long-term conservation ecology, conservation genetics, and population biology research program on northeastern Türkiye's large carnivores (brown bears, wolves, and lynx) conducted by the KuzeyDoğa Society since 2006 (Akkucuk and Şekercioğlu 2016), in a country where habitats and biodiversity are under immense human pressure (Şekercioğlu et al. 2011a, b). The study area was located on the Kars-Ardahan high plateau (903–3427 m a.s.l.) in northeastern Türkiye (Fig. 1, Supporting information). The core study area (~ 550 km^2; 40°20'N, 42°35'E) included the Sarıkamış-Allahuekber Mountains National Park (hereafter SAMNP) and the surrounding forests. The city of Sarıkamış (population: ca 15 500 in 2023) is in the center of the study area (Turkish Statistical Institute 2024). The SAMNP is located north of the city, while the remainder of the forest is to the south, divided from the SAMNP by a major road (Fig. 1). The SAMNP covers an area of 225.2 km^2, but only 22% or 49.69 km^2 is forested (Capitani et al. 2016). The core study area consists solely of the forests surrounding the city of Sarıkamış, where all of the wolves were initially captured, and all camera trapping took place. This core area ranges in elevation from 1900 to 3120 m a.s.l. and is composed of 328.38 km^2 of fragmented forest, in a matrix of agricultural and rangelands (Chynoweth 2017). The logging and forest loss has increased substantially since 2019 (Global Forest Watch 2023). All wolves at least partially utilized areas outside the 'core' study area which is fully described in the Supporting information.

Most of the forest cover in the region is composed of Scots pine *Pinus sylvestris,* accompanied by small patches of European aspen *Populus tremula*. It is legally logged yearly, with the intensity of logging increasing from an average of 4 ha/year from 2015 to 2019 to almost 38 ha/year since 2020, resulting in a forest cover decrease of 1.1% since 2020 (Zhang et al. 2020, Global Forest Watch 2023). Understory vegetation is scarce due to extensive domestic livestock grazing, firewood collection, and other human use. The climate is continental, with temperate summer months from June through September (average monthly: 13–18°C) and cold winter months with snowfall from November through March (average monthly: −10 to 0°C; Cozzi et al. 2016). Outside the harsh winter months, humans are heavily present in the forest, both spatially and temporally. Human activity is mostly limited to livestock grazing, legal and illegal timber harvest, and recreation. Livestock in the area is composed of cattle, sheep, and goats freely roaming in rangelands and pastures from April to November (Capitani et al. 2016). In the summer, 41% of the wolves' diet in this region comes from livestock, while the other 59% of the diet is made up of squirrels *Sciurus vulgaris*, rodents, wild boar *Sus scrofa*, and hare *Lepus europaeus* (Capitani et al. 2016). Snow-tracking censuses showed a density of 3.0 wolves per 100 km^2 (range: 1.2–6.4) in the forests surrounding Sarıkamış town (Kusak 2022).

Camera trapping

To understand how camera detection rates and activity patterns of human presence differ across seasons, we used camera traps deployed in the forests surrounding Sarıkamış between



Figure 1. A map of the study area and its location within Türkiye. The blue line represents the 95% home range of all non-dispersing wolves. The boundaries of the Sarıkamış-Allahuekber Mountains National Park (SAMNP) are in turquoise. Sarıkamış is the urban area south-east of the SAMNP.

2018 and 2023 (Blount et al. 2021). The core study site was segmented into 2 km^2 grid cells. A combination of Keepguard and Reconyx cameras (Keepguard KG891, Reconyx PC900, Reconyx HPX2) was used. Camera locations were randomly chosen from these grid cells, and cameras were deployed within selected grid cells along dirt roads (Naderi et al. 2021). All cameras were placed on trees at a height of approximately 3 m and pointed down at a roughly 45° angle. Cameras were left in the field for an average of 96 days (range: 7–728 days), at which point they were moved to another randomly selected grid cell. Cameras active for fewer than seven days were excluded to avoid data bias. Cameras were programmed to take photos with no reset interval between triggers, and the sensitivity was set to 'high'. Each camera was set to operate for 24 h a day. No bait was used at any sites.

Camera detection rate

Photos from camera traps were uploaded and identified with Wildlife Insights (WildlifeInsights.org). A matrix composed of the dates each camera was active was created using the R package 'camtrapR' (Niedballa et al. 2016). Images were then subset to include only independent events. Independent events were considered photos with a time difference greater than 60 seconds between detections of the same species at the same site (Cove et al. 2021). Timestamps for photos and cameras were changed into Julian day and grouped by day rather than year. Detection rate was then calculated by dividing the number of detections of each species or group by the number of cameras active during that day. Human presence was defined as the detection of humans, cattle, or vehicles. A Welch two sample t-test with a Bonferroni adjusted p-value was used to determine the difference in detection rate between pup-rearing and nomadic seasons.

Wolf capture and collaring

Wolves were captured from 2011 to 2022 using foothold traps (Livestock Protection Company, Alpine, Texas, US; LPC #7 EZ GRIP) in the forests surrounding the city of

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Sarıkamış, following the procedure described in Kusak et al. (2005). Immobilized wolves were fitted with GPS/GSM or GPS/Iridium tracking collars (GPS Plus and Vertex LITE; Vectronic Aerospace GmbH, Berlin, Germany), which were programmed to record one GPS fix every five or six hours. The sex, reproductive status, and age of each wolf were determined and recorded while the wolf was sedated. Age was assessed on the basis of body size and tooth wear (Gipson et al. 2002).

Data preparation

Only wolves with GPS data with acquisition rates of > 90% that stretched at least 30 days during a full season (Supporting information) were included in the study. In addition, erroneous GPS points taken at intervals of less than five hours or more than six hours were excluded in order to create a uniform time interval between points.

Determination of the seasonal cycles

The dates for the seasonal cycles were based on life history and breeding information. We separated each year into two seasons: the pup-rearing season (1 April–30 September) and the nomadic season (1 October–31 March). The pup-rearing season is defined by the beginning of the whelping season, which is estimated to start in April. The nomadic season of territorial wolves is marked by a decreased use of the rendezvous sites, changes in food availability, and the presence of pups on hunts with adults, all of which may affect wolf behavior and habitat selection (Person 2001, Mech and Boitani 2003). Individuals whose data stretched multiple years were counted as different individuals in each year (e.g. if a wolf was tracked from May 2020 to July 2021, its data would be used in the pup-rearing season for 2020, the nomadic season for 2020, and the pup-rearing season for 2021; Levin 2020).

Determination of residency status

Residency status of wolves was determined by identifying their movement pattern with the net squared displacement (NSD) approach (Clobert et al. 2012, Singh et al. 2012) with the R packages 'migrateR' (Spitz et al. 2017, Spitz 2019) and 'amt' (Signer et al. 2019). Net squared displacement is a robust method to characterize individual movement patterns based on distance between continuous locations (Bunnefeld et al. 2011, Singh et al. 2012, 2016) that has been successfully used to determine the residency status of wolves (van den Bosch et al. 2023). Resident individuals with stable home ranges are identified through an asymptotic NSD curve over tracking time, while dispersers present a sigmoid NSD curve (Clobert et al. 2012). Animals that shifted from one residency status to the other during a season were excluded for that season as they violated the assumptions of an individual being a range resident (i.e. the tendency of an animal to remain within its home range: Mueller and Fagan 2008, Silva et al. 2022).

Home range analysis

Home range analysis has traditionally relied on the assumption of independent and identically distributed (IID) data (Worton 1989, Silverman 1998, Noonan et al. 2019). However, the use of GPS collars with much shorter relocation intervals than triangulation techniques introduces inherent autocorrelation, which can greatly underestimate home range sizes (Fleming et al. 2015, Fleming and Calabrese 2017). To mitigate the effects of autocorrelation on home range calculations, home ranges were calculated using an pHREML ADKE ('ctmm', R Package, Calabrese et al. 2016), using the processes described in Fleming et al. (2015), Calabrese et al. (2016), Fleming and Calabrese (2017), Morato et al. (2018), Noonan et al. (2019) and Silva et al. (2022). Home ranges were also calculated using the kernel density estimator method (KDE) using the workflows described in the production of the pHREML AKDE home range. Both 95 and 50% isopleths were calculated to understand entire and core activity. See the Supporting information for a more detailed overview of the method used for these analyses.

To investigate the effect that season, residency status, and human presence could have on home range size, we used a linear mixed-effect model (LMM, 'lme4' R package, Bates et al. 2015) with individual ID as a random effect. For the first model, we used a subset of home range data (50 wolf seasons) that had corresponding camera trap data (2018–2023). Generally, pack ID is used instead of the individual ID as the random intercept to account for the hierarchical structure of wolves within packs (Hebblewhite and Merrill 2008). However, as our data covered several seasons and years, wolves may have changed residency status between years. Therefore, we decided to use the individual ID. The estimated home range for each wolf was log transformed and used as the response variable. The first model consisted of log transformed home range as the response variable, with season, residency status, and human presence as predictor variables, and individual ID as a random effect. As human presence was not significant (Results), we ran a second model, omitting human presence, where we were able to include all available home range data (80 wolf seasons of 31 individuals). In this model, we used log transformed home range size as the response variable, with season and residency status as predictor variables and individual ID as a random effect. The 95% confidence interval for each variable was calculated using a bootstrapped estimate of SE (Efron 1979, DiCiccio and Efron 1996), and both confidence intervals and home range estimates were back transformed for the results.

Finally, wolves with home ranges that were calculated in the same season across multiple years were assessed to understand how constant home range sizes were between years, and to understand how home range sizes may vary as a wolf changes from a resident to a non-resident. Significance was assessed by comparing overlap of the 95% confidence intervals of home range size between individuals.

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Activity patterns

Activity patterns were assessed using the accelerometer data for wolves and the camera trap photos for human presence. Accelerometer data were collected after the collars were retrieved. Since accelerometer data can be inconsistent across individuals due to external variation (e.g. collar snugness), the activity cut-off for each accelerometer must be calculated individually (Gervasi et al. 2006). Accelerometer data were recorded from 0 to 255 in both the X and Y planes and averaged across five-minute periods. A binomial activity pattern was constructed by combining the accelerometer data from the X and Y planes, binning the data in 51 activity classes of 10 units, and plotting the resulting data on a histogram (Gervasi et al. 2006). The trough between the initial zero-inflated peak and the first local maximum was determined to be the 'cutoff' of activity, where numbers lower than the cutoff were considered inactive and those above the cutoff were considered 'active' (Gervasi et al. 2006).

Activity patterns for human presence were calculated using the first recorded time for each independent event as 'active' times. Activity patterns and relative abundance measurements (detection rate) for human presence were the only use of camera trap data in this study. All data describing the activity of wolves came from GPS collars.

With these data, we tested whether wolf temporal activity changed across both seasons and residency status. Then, we tested how the activity overlapped between resident wolves and human presence changes between seasons. Before analysis, all detections were transformed to solar time (Wutzler 2021). Wolves were separated by residency status and seasons, but there was no minimum requirement for collared time to be included in the total dataset. However, if an animal was not collared long enough to determine residency status, its data were simply used for seasonal differences.

We compared activity distributions (or 'overlap') across groups using circular kernel density analysis in the package 'overlap' (Meredith and Ridout 2014). First, we calculated the coefficient of overlap (Δ_1) between each pairwise comparison as a relative measure of the magnitude of the difference between groups, and we used information from 10 000 empirical bootstrap resamples to calculate 95% confidence intervals (CI). To assess for significant differences in distributions, we used Watson's two-sample test of homogeneity (Rao and Sengupta 2001, Agnostinell and Lund 2017), with $\alpha = 0.05$, for each pairwise comparison. In Sarıkamış, 42% of all resident relocations were within the forest (the core study system). This number increases to 66% of all resident points when relocations within 1 km of the forest edge are included, while disperser wolves spend a majority of their time outside the core study system (82% of relocations are outside the core study forests). Furthermore, almost all of the known pup-rearing, rendezvous, and other biologically important sites for resident packs are within the forest surrounding Sarıkamış (Blount, Kusak and Şekercioğlu, unpubl.). Therefore, to understand how the changes in human presence affect wolf activity patterns, we compared human presence measured with camera traps within forests to the accelerometer data for resident wolves only. We decided to use camera trap data to measure human presence, as most of the human activity within forests takes place on or near roads (Blount, Kusak and Şekercioğlu, unpubl.). Furthermore, since wolf activity measured by camera traps would only describe when wolves use roads, and not their total activity, we used the full extent of the accelerometer data of the resident wolves in this comparison.

We grouped the detections of wolves into the following time periods: twilight (detections occurring one hour before and after both sunrise and sunset), daytime (detections occurring more than one hour after sunrise and one hour prior to sunset), and night-time (detections occurring more than one hour after sunset and one hour prior to sunrise). We used 'twilight' as a proxy of crepuscular activity, and therefore used a more expanded definition in order to capture all potential activity linked to crepuscular behavior (Green et al. 2023). All of the analyses were conducted using the 'activity' (Rowcliffe 2014) and 'circular' (Agnostinell and Lund 2017) packages in R.

We calculated the total activity (i.e. the proportion of the day spent active) for each comparison group, using the same bootstrapping method as above to calculate the 95% CIs (Rowcliffe 2014). We looked for significant changes across comparison groups by comparing the overlap of the resultant CIs. If CIs did not overlap, then we considered that a 'statistically significant' difference was found in activity across comparison groups. In addition, we calculated the 50% isopleth for each comparison group (i.e. the shortest time interval containing 50% of all detections) using the methodology developed by Oliveira-Santos et al. (2013), which we refer to hereafter as 'core activity'.

Finally, using the 'Diel.Niche' R package (Gerber et al. 2023), we tested whether our comparison groups maximized their diel activity during the daytime, night-time, or twilight hours (i.e. which time period was used the most) by modeling the number of detections within each time group and comparing the CI of each group with the amount of time 'available' within each period. A failure of the CI to overlap the 'available time' was considered a significant difference. Furthermore, if a particular time of day was 'used' more than available, then we classified that as 'selection' for that period of the day. We classified 'avoidance' as time periods 'used' less than their availability (Gerber et al. 2023). All statistical analyses and graphing were conducted in R (ver.4.2.2, 2022-10-31; www.r-project.org).

Results

Camera detection rate

From 2018 to 2023, we used cameras at 142 different sites, which were active for 19 137 trap nights, producing 286 874 photos with 12 312 detections of human presence. See Supporting information for total counts per season

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and detection rate per camera per day of each species and group. We considered the nomadic season as the baseline and assessed all changes between seasons relative to it. For all groups, the camera detection rate rose significantly in the pup-rearing season compared to the nomadic season. People increased their use of the forest by 356% (Fig. 2), increasing the average detection rate from a baseline of 0.060 detections of people per camera per day to 0.214 humans per camera per day ($p < 0.001$). This trend was paralleled by vehicles, whose presence in the forest increased by 360% from 0.222 to 0.800 vehicles per camera per day ($p < 0.001$). The presence of livestock in the forest, which are always guarded by people and typically dogs (Kusak and Şekercioğlu 2021), had the largest increase (409%), going from 0.021 detections per camera per day to 0.086 ($p < 0.001$, Fig. 2, Supporting information).

Home range size

In total, 89 tracks for 89 wolf seasons were calculated from 31 tracked wolves (Supporting information). Data from nine seasons were excluded based on violation of range residency ($n = 1$), insufficient duration of being collared ($n = 5$), and low effective sample size ($n = 3$), leaving an effective sample size of 80 wolf seasons representing 30 wolves. In all, 20 wolves representing 50 wolf seasons (31 residents, 19 non-residents; Supporting information) were used to analyze the effects human presence have on home range size, as the remaining 30 wolf seasons did not have information on human presence. Only residency status was a significant predictor of home range size ($p > 0.001$). Human presence did not significantly explain the differences in home range size ($p = 0.367$, 95% aKDE), nor did season ($p = 0.919$, 95% aKDE). Since human presence did not affect home range size, a final model was run with the full dataset of home range sizes (80 wolf seasons from 30 individuals, 28 non-resident seasons, and 52 resident seasons; Supporting information). As with the previous model, only residency status was significant for all home range estimates (Table 1). Home range size (95% aDKE) in the pup-rearing season grew from 322 km^2 for resident wolves to 1121 km^2 for non-resident wolves. Likewise, in the nomadic season, resident wolves (211 km^2) had smaller home ranges than non-resident wolves (1169 km^2). These trends were similar in each home range estimator and for core and whole home ranges (Fig. 3). Table 2 provides the aKDE- and KDE-derived 95% whole and 50% core home range for residents and non-residents in each season.

Within-individual variability in home ranges

To understand the within-individual variability in home ranges we compared how individual wolves changed the size of their 95% aKDE home range size 1) in the same season across multiple years, and 2) across seasons in the same year. Over the course of the study, 20 wolves were present for the same sampling periods over multiple years (Supporting information). Of these, nine wolves had two years of the same season where they had the same residency status, eight wolves had two years of the same season where they did not have the same residency status, and three wolves were included in both groups because they had two years of the same season where they had the same residency status and a third year of the same season where they had a different residency status. For the 12 wolves with two years of data from the same season where they did not change residency status, seven significantly changed their home range size. None of the dispersers had significantly different home range sizes, while six of the nine resident wolves did. For the 11 wolves that had data

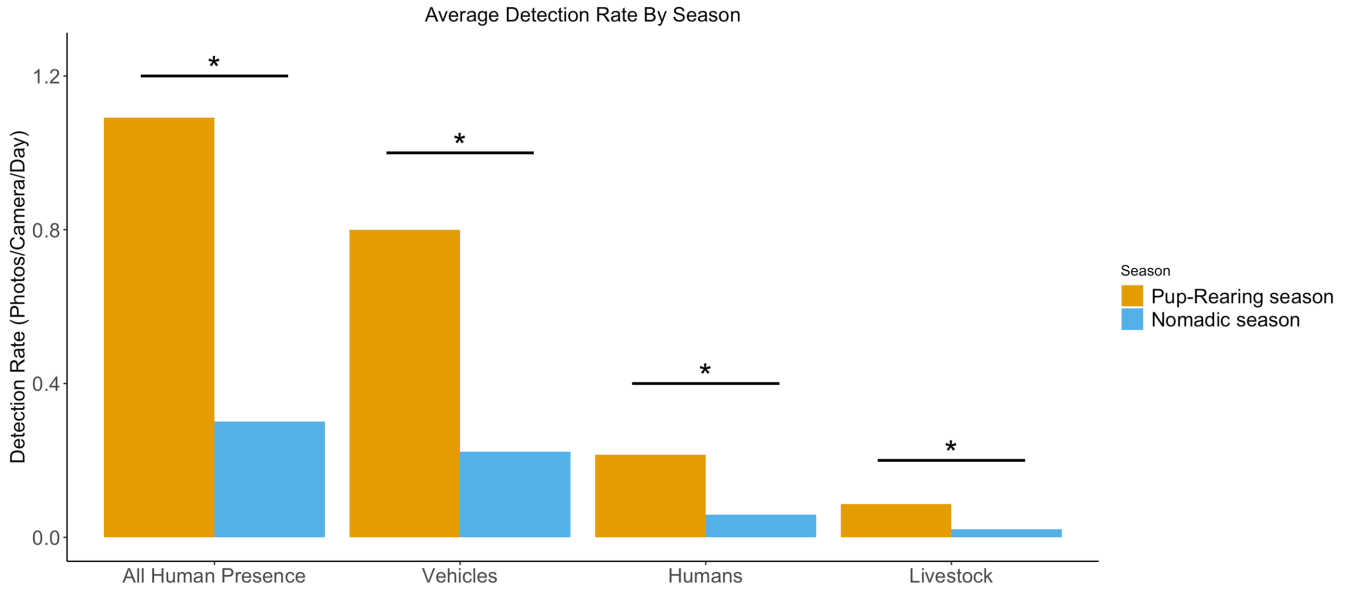


Figure 2. Average detection rate for each disturbance type in the pup-rearing and nomadic seasons. Detection rate was calculated per camera per day and averaged across the full array. Significance ($p < 0.05$) is denoted by *. All seasons were significantly different.

Table 1. Results of the linear mixed-effects model used to investigate the effect of season and residency status on home range estimation. Individual ID was used as a random effect. Intercept reflects the values of non-resident in the nomadic season. Regression coefficient is presented alone while standard error is presented in parentheses and significance is denoted by asterisks ***. In all cases of significance $p < 0.001$.

	Intercept	Season	Residency status	Interaction
95% AKDE	7.06 (0.35)***	−0.04 (0.41)	−1.71 (0.43)***	0.47 (0.52)
95% KDE	7.15 (0.30)***	−0.48 (0.32)	−1.43 (0.35)***	0.01 (0.41)
50% AKDE	5.27 (0.42)***	0.16 (0.48)	−1.86 (0.51)***	0.48 (0.61)
50% KDE	5.47 (0.32)***	−0.44 (0.33)	−1.53 (0.37)***	−0.23 (0.42)

from the same season in different years and different residency status, the home range sizes for nine were significantly different. Of these, seven had larger home ranges when they were dispersers.

There were 21 wolves whose home range sizes were recorded in both seasons of the same year. Of these, five were non-residents and 16 were residents. Of these 21 wolves, 14 (two non-residents and 12 residents) had significant changes. Both non-residents had larger home range sizes in the nomadic season than the pup-rearing season, as well as nine of the 12 residents.

Activity patterns – wolves

From 2011 through 2023, we recorded 578 546 activity measurements from 19 wolves across 54 seasons. This number is different from the number of tracked wolves, as we had to recover the collar in order to access the activity data. We recorded 145 077 measurements during the nomadic season (n = 17, seven non-residents and 10 residents) and 433 469 measurements during the pup-rearing season (n = 34, 11 non-residents and 23 residents). We recorded 219 990 measurements from 18 dispersing individuals (62 808 during the nomadic season and 157 182 during the pup-rearing season), and 352 921 from 33 resident individuals (80 587 during the nomadic season and 272 334 during the pup-rearing season). Average proportional availability of daytime, night-time, and twilight hours was 0.41, 0.42, and 0.17, respectively. See Supporting information for the number of detections in each category.

All comparison groups exhibited different temporal activity distributions from each other, although the relative



Figure 3. Core and whole home ranges (50, 95%) calculated using pHREML AKDE and KDE of wolves with different residency status and across seasons. Mean for each group is denoted by a translucent circle and lines represent the 95% confidence interval. For each calculation method, there was a significant difference ($p < 0.001$) between the residency status for each season (i.e. Non-resident pup-rearing versus Resident pup-rearing) denoted by *. Orange and blue lines above home range estimates denote season for significantly different home range sizes (orange connects the pup-rearing seasons, and blue lines connect the nomadic season).

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Table 2. Back transformed estimates of home range sizes from the results of the linear mixed-effects model. In each case, individual ID was used as a random effect. Confidence intervals are provided in parentheses and were calculated with a bootstrapped estimate of error.

		Pup-rearing season				Nomadic season			
	Residency status	Resident		Non-Resident		Resident		Non-Resident	
	Size	Core 50%	Whole 95%	Core 50%	Whole 95%	Core 50%	Whole 95%	Core 50%	Whole 95%
pHREML aKDE		57 km^2 (8–422 km^2)	322 km^2 (73–1554 km^2)	227 km^2 (74–749 km^2)	1121 km^2 (379–3469 km^2)	30 km^2 (8–107 km^2)	211 km^2 (63–486 km^2)	194 km^2 (89–437 km^2)	1169 km^2 (614–2407 km^2)
KDE		26 km^2 (6–113 km^2)	190 km^2 (46–708 km^2)	153 km^2 (62–381 km^2)	784 km^2 (337–1823 km^2)	52 km^2 (20–131 km^2)	303 km^2 (121–766 km^2)	239 km^2 (131–452 km^2)	1269 km^2 (714–2274 km^2)

magnitude of the changes was low (Fig. 4, Table 3). Nomadic season distributions differed from pup-rearing season distributions both overall and within each residency status category, with overlap being relatively high across comparisons ($D_{nomadic_vs_pup\text{-}rearing|all_data} = 0.93$, CI = 0.91–0.94, $p < 0.001$; $D_{nomadic_vs_pup\text{-}rearing|non\text{-}resident} = 0.93$, CI = 0.91–0.93, $p < 0.001$; $D_{nomadic_vs_pup\text{-}rearing|resident} = 0.92$, CI = 0.91–0.93, $p < 0.001$). Likewise, distributions across residency status also differed from each other both overall and within each season, but overlap was again relatively high across comparisons ($D_{non\text{-}resident_vs_resident|all_data} = 0.95$, CI = 0.94–0.96, $p < 0.001$; $D_{non\text{-}resident_vs_resident|nomadic} = 0.94$, CI = 0.93–0.95, $p < 0.001$; $D_{non\text{-}resident_vs_resident|pup\text{-}rearing} = 0.95$, CI = 0.95–0.97, $p < 0.001$).

Wolves spent significantly less time active per day during the pup-rearing season (mean = 0.54, CI = 0.51–0.56, Fig. 5, Table 4) than during the nomadic season (mean = 0.58, CI = 0.55–0.60) overall ($p = 0.046$). Furthermore, non-resident wolves spent less time active per day than did residents in the non-breeding season ($mean_{non\text{-}resident|nomadic} = 0.53$, CI = 0.50–0.54; $p = 0.021$), but this difference was not significant for all other comparisons.

Core activity did not differ significantly across groups (Fig. 6, Table 5). Seasonal changes in core activity differed more than the changes across residency status (nomadic season core activity = 22.20–5.95 h [7.75 total hours]; pup-rearing season core activity = 22.42–6.86 h [8.44 total hours]; non-resident core activity = 22.10–5.93 h [7.83 total hours]; resident core activity = 22.33–6.53 h [8.20 total hours]). Both residents and non-residents shifted to shorter, more nocturnal core activity in the nomadic season (non-resident nomadic season core activity = 22.22–5.63 h [7.41 total hours]; non-resident pup-rearing season core activity = 21.57–6.54 h [8.97 total hours]; resident nomadic season core activity = 22.33–6.18 h [7.85 total hours]; resident pup-rearing season core activity = 22.50–6.97 h [8.47 total hours]).

All comparison groups selected for night-time activity and avoided daytime activity (Fig. 7, Table 6; all posterior probabilities of night-time maximization = ~100%). Furthermore, there was either evidence for minimal avoidance or no selection of twilight activity across all comparison groups. When all groups were combined, wolves were more active at night during the nomadic season ($mean_{nomadic} = 0.73$, CI = 0.72–0.73) than during the pup-rearing season ($mean_{pup\text{-}rearing} = 0.48$, CI = 0.48– 0.48). Correspondingly, wolves were more active in the daytime during the pup-rearing season ($mean_{pup\text{-}rearing} = 0.31$, CI = 0.31–0.31) than during the nomadic season ($mean_{nomadic} = 0.15$, CI = 0.14–0.15). In addition, wolves were more active at twilight during the pup-rearing season ($mean_{pup\text{-}rearing} = 0.21$, CI = 0.21–0.21) than during the nomadic season ($mean_{nomadic} = 0.13$, CI = 0.13–0.13). This trend in activity was found for both dispersing individuals and resident individuals, with a larger difference occurring among resident individuals (Fig. 7, Table 6). This is supported by comparisons of diel activity distributions (Fig. 4).

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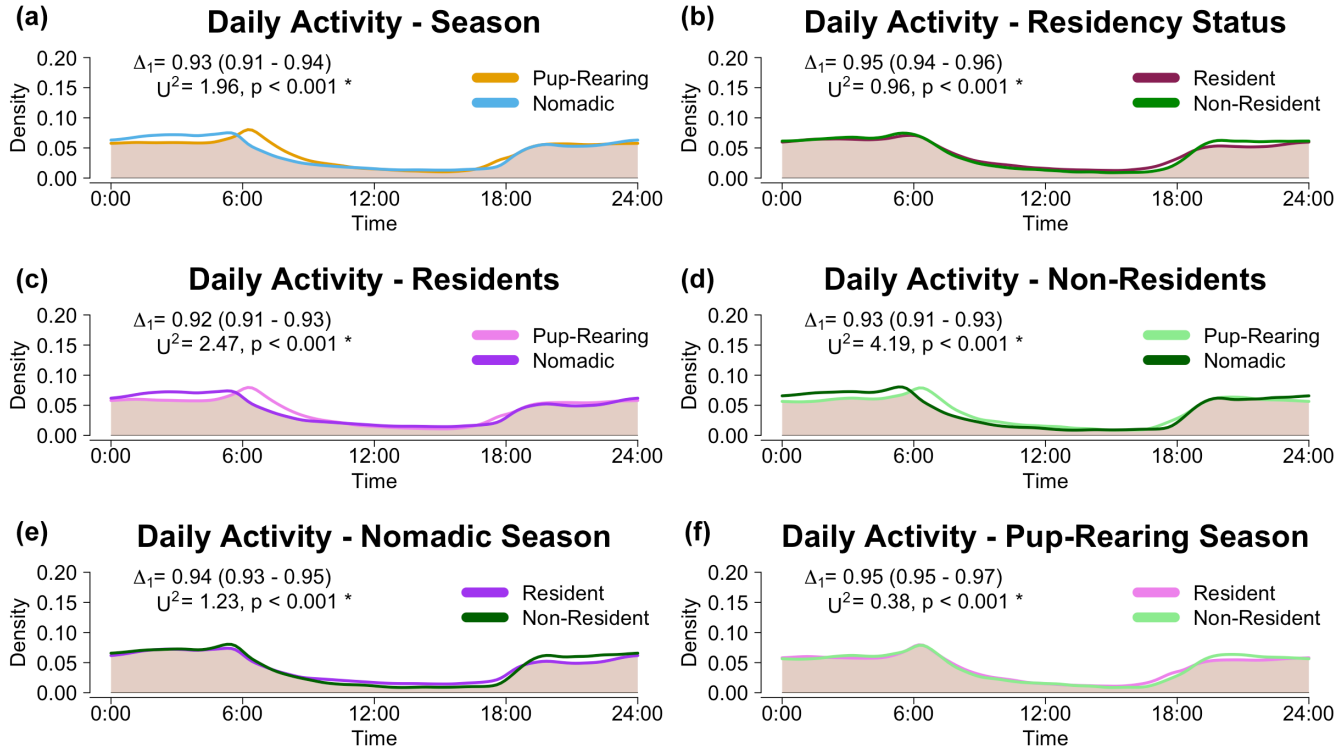


Figure 4. Diel activity distribution comparisons across seasons (a), (c), and (d) and residency status (b), (e), and (f). Curves represent the smoothed kernel density distribution for each population. The shaded region represents the area under which both curves overlap. The estimated overlap coefficient and associated 95% confidence intervals are shown in the top line, with the results of Watson's two-sample test of homogeneity shown below.

Changes in overlap of activity patterns between wolves and humans

Comparisons between wolf and human activity were made exclusively with the data from resident wolves. Therefore, wolf data comprised 352 921 active points from 33 wolf seasons from resident individuals (80 587 during the nomadic season and 272 334 during the pup-rearing season). Together with the data from camera traps (Fig. 8), we were able to understand the differences in overlap between wolves and people between seasons.

Overlap with people was greater in the nomadic season ($D_{wolf_vs_anthropogenic|nomadic} = 0.47$, CI = 0.44–0.46, $p < 0.001$) than in the pup-rearing season ($D_{non\text{-}resident_vs_resident|all_data} = 0.26$, CI = 0.33–0.35, $p < 0.001$).

Discussion

In the first wolf tracking study in Türkiye, we investigated the patterns in diel activity and trends in home range sizes for wolves in a human-dominated ecosystem. We showed that human presence in wolf habitat was much lower in the nomadic season for resident wolves and increased by 356% in the pup-rearing season. Contrary to our original hypothesis, we detected no difference between seasons for both core and entire (50% and 95%, respectively) home range sizes, despite a three- to four-fold change in human presence. As expected, non-resident wolves had significantly larger home range sizes than did resident wolves across all scales and seasons. While the activity patterns of wolves were similar between seasons, resident wolves had greater overlap with humans and were

Table 3. Comparison of overlap of temporal activity distributions between groups. Overlap is the magnitude of the difference between the activity distribution of both groups. Confidence intervals (CI) calculated using 10 000 empirical bootstrap resamples and the result of a Watson's two-sample test (U^2) of homogeneity is also included. The Watson's two-sample test, with an $\alpha = 0.05$, compares each of the groups to see if they are significantly different from each other. In all cases, the p value from the U^2 was less than 0.001 and is denoted by *.

Group 1	Group 2	Overlap (CI)	U2
Nomadic – All	Pup-Rearing – All	0.93 (0.91–0.94)	3.2*
Non-Resident – All	Resident – All	0.95 (0.94–0.96)	1.75*
Nomadic – Resident	Pup-Rearing – Resident	0.93 (0.91–0.93)	4.22 *
Nomadic – Non-Resident	Pup-Rearing – Non-Resident	0.92 (0.91–0.93)	1.82*
Nomadic – Non-Resident	Nomadic – Resident	0.94 (0.93–0.95)	0.94*
Pup-Rearing – Non-Resident	Pup-Rearing – Resident	0.95 (0.95–0.97)	0.31*

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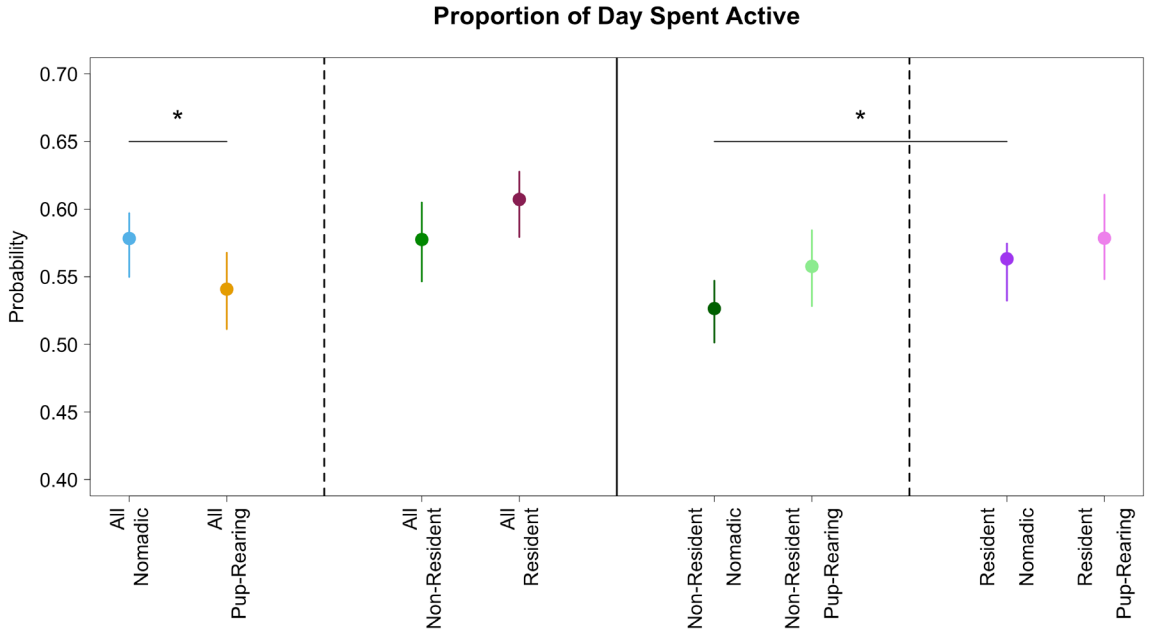


Figure 5. Estimated proportion of time spent active across comparison groups. Each point corresponds to the mean estimate, with error bars corresponding to bootstrapped 95% confidence intervals. * represents significance based on confidence intervals.

more active than non-residents when humans were less present in the landscape. These results suggest that wolves may, to a small degree, change their activity patterns but not their home range size to take advantage of fluctuations in the perceived threat from people. However, some of this wolf activity results from an increase in nocturnality even though human presence in the forest was already at its lowest during the year. Therefore, understanding the drivers of this increased nocturnality in the nomadic season may explain how wolves have adapted to this system, and how they may adapt to similar situations across their distribution range. A possible explanation of increased wolf nocturnality during the nomadic season may be their dependence on human food sources. This is especially true during winters, where wolves have been reported to search for food in and around villages at night (Kusak and Şekercioğlu, unpubl.).

Changes in home range size between and among groups across seasons

In the first GPS telemetry study on wolves in Türkiye, we showed that the pHREML aKDE mean home range of resident wolves in our system was 322 km^2 in the pup-rearing season and 211 km^2 in the nomadic season. While home ranges calculated using pHREML aKDE may produce the best estimates for wolves in this region, to make the data comparable to other studies we also calculated home ranges with KDE. Using KDE, we showed the estimated 95% home range size of resident wolves to be 190 km^2 in the pup-rearing season and 303 km^2 in the nomadic season. The 50% core home range was 26 km^2 in the pup-rearing season and 52 km^2 in the nomadic season. The KDE calculated core and full home ranges we found are in line with the estimates produced by other similar studies. The home ranges of wolves in this study area were found to be smaller than some studies (95% to 708 km^2 – Scandinavia, Mattisson et al. 2013) but larger than others (95% to 104 km^2 – Italy, Mancinelli et al. 2018; 50% to 15.5 km^2 – Poland, Okarma et al. 1998; 50% to 26.2 km^2, 3.3 km^2 – Croatia, Kusak et al. 2005). The aKDE-calculated home range sizes of wolves in the nomadic season were smaller than in the pup-rearing season, which contrasts with similar studies (Okarma et al. 1998, Kusak et al. 2005). This was only shown in aKDE-estimated home ranges and not the more traditional KDE-estimated home ranges (Table 2). As this is one of the first studies to use aKDE to adjust for spatial autocorrelation in wolves, further investigation is needed

Table 4. Total time spent active per day by each subgroup. The mean proportion of time spent active per day and their associated confidence intervals (CI) from 10 000 empirical bootstrap resamples. Significance between groups is denoted by A and B.

Residency status	Season	Mean (CI)	Significance
All	Pup-Rearing	0.54 (0.51–0.56)	A*
All	Nomadic	0.58 (0.55–0.60)	A*
Resident	Pup-Rearing	0.58 (0.55–0.61)	
Resident	Nomadic	0.56 (0.53–0.57)	B*
Non-Resident	Pup-Rearing	0.56 (0.53–0.59)	
Non-Resident	Nomadic	53 (0.50–0.54)	B*

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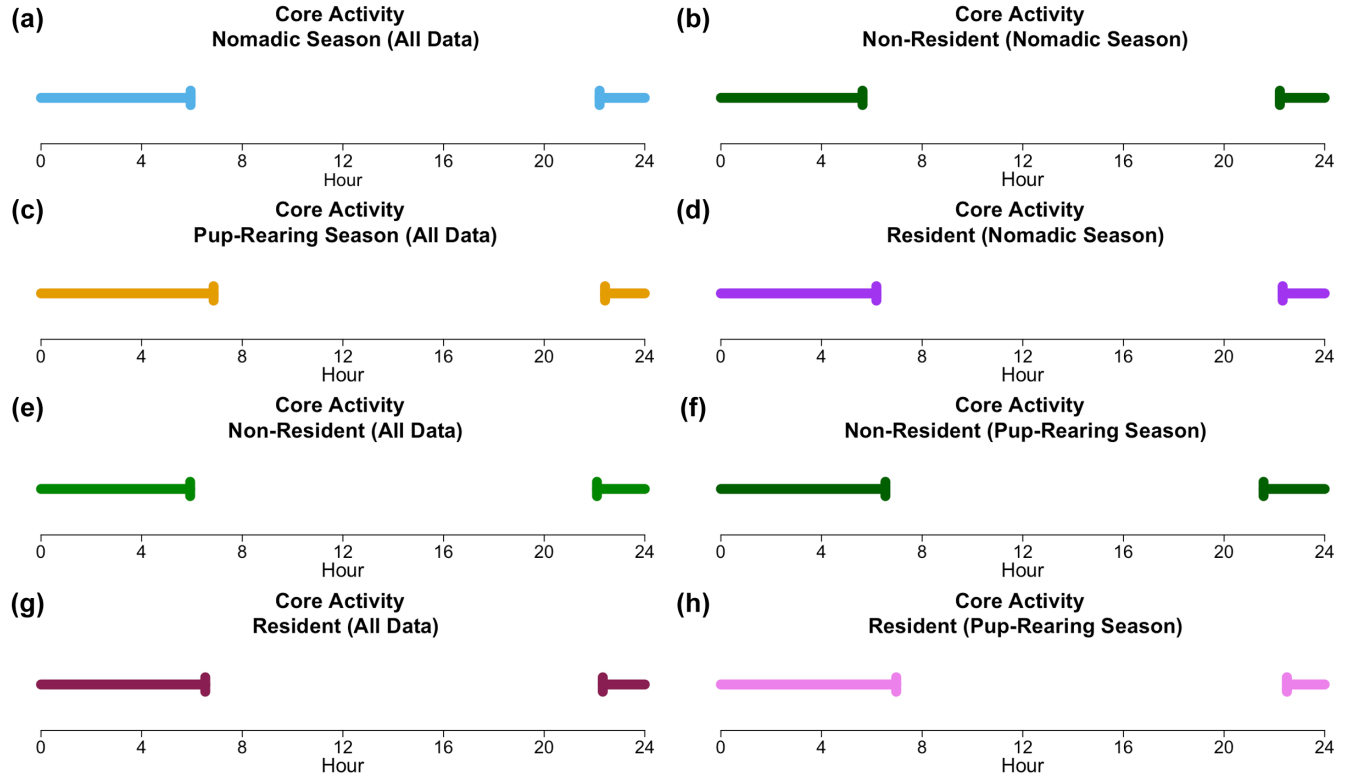


Figure 6. Core diel activity across seasons for all wolves (a), (c); across residency status within the nomadic season (b), (d); across residency status for all seasons (e), (g); and across residency status within the pup-rearing season (f), (h). Segments represent the shortest time interval containing 50% of all detections.

to understand if this is representative of autocorrelated corrected home range sizes, or if it is unique to this system. This finding may indicate the dependency of wolves on human food sources which, during long winters in the area, is concentrated around villages (Kusak and Şekercioğlu 2021). It is important to note that the differences found between seasons were not significantly different.

Wolf home ranges can be shaped by many external factors, including top-down and bottom-up pressures (Ballard et al. 1987, Wydeven et al. 1995, Okarma et al. 1998, Mech and Boitani 2003, Jedrzejewski et al. 2007, Mattisson et al. 2013, Kittle et al. 2015, Petroelje et al. 2019). Anthropogenic disturbances like roads and settlements are concentrated in the center of our study system and are not homogeneously distributed in the landscape (Fig. 1). This means habitats closer to the center of the study system, which are mainly used by resident wolves, may be more fragmented than further habitats used by non-residents. Analysis of habitat selection within home ranges may shed light on how anthropogenic factors and human presence shape home range size, and may help explain the high variability in home range size of resident wolves.

Our findings that home range size did not change between seasons are consistent with similar studies (Mancinelli et al. 2018). Lack of seasonal variability in home range size has often been tied to non-migratory prey (Fuller 1989, Hayes et al. 1991, Mancinelli et al. 2018). In the summer, the diet of these wolves is composed of up to 40% livestock and 60% small- to medium-sized mammals. While the winter diet of wolves in this region has yet to be assessed,

Table 5. Duration of core activity of animals in each residency status and season. Start and end of core activity are denoted in 24-h time notation. Core activity calculates the smallest amount of time that comprises 50% of the total activity.

Residency status	Season	Start core activity	End core activity	Duration of core activity (Hours)
All	Pup-Rearing	22:25	6:52	8:26
All	Nomadic	22:12	5:57	7:45
All	Resident	22:20	6:32	8:12
All	Non-Resident	22:06	5:56	7:50
Resident	Pup-Rearing	22:30	6:58	8:28
Resident	Nomadic	22:20	6:11	7:51
Non-Resident	Pup-Rearing	21:34	6:32	8:58
Non-Resident	Nomadic	22:13	5:38	7:25

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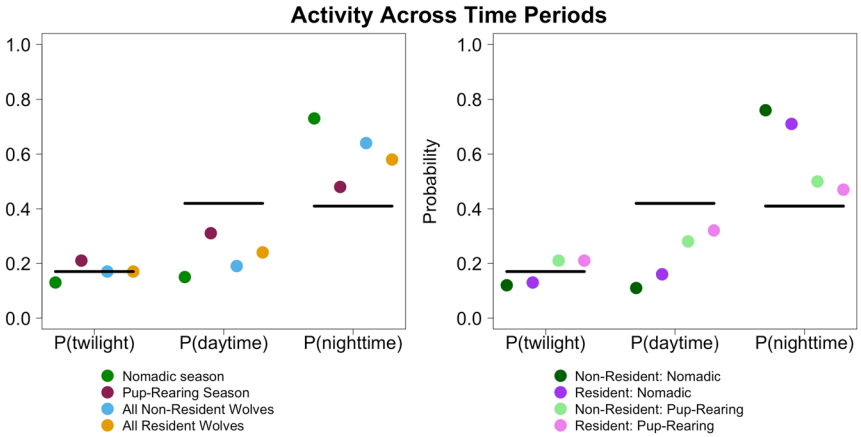


Figure 7. Probability of activity during different time periods across residency status and seasons. Points represent mean estimates for the proportion of time spent active within each time period. Bayesian 95% credible intervals not shown because they do not extend beyond the points. Black lines represent the mean proportion of time 'available' within each time period. All comparisons are significantly different aside from twilight activity of all non-resident wolves and all resident wolves, and twilight activity of non-resident pup-rearing wolves and resident pup-rearing wolves (Table 6).

livestock, which makes up to 40% of the summer diet, is less readily available in this region in the winter (Capitani et al. 2016). Since wolves in this system did not change their home range size, even with a possible shift in diet, this may suggest wolves in human-dominated systems establish home ranges large enough to account for seasonal variation in resources (Mancinelli et al. 2018). However, further investigation into the winter diets of these wolves is needed.

Many of the studies done in human-dominated areas of southern Europe have used small numbers of tracked wolves to understand home range size (Mancinelli et al. 2018). Based on the tracking of 31 wolves across 80 seasons, we show that wolves in our system exhibited a high degree of variation in home range size across seasons and years. This was particularly evident for resident wolves, which significantly changed their home range size 66% of the time between years; and 75% changed home range size between seasons. Even though many individual wolves altered their home range size, population-level estimates of home range sizes between seasons were not significantly different. This result highlights the need for large datasets to understand how wolves may react at the population level and for further investigation of the drivers affecting the differences of home range size among individuals.

Non-resident wolves, on the other hand, did not significantly adjust their home range size between seasons or years. While the sample size was lower for non-residents than residents, no non-resident wolves (n = 2) changed their home range size between years, and only 40% (n = 5) changed between seasons. This discrepancy may be due to non-resident wolves having left higher-quality habitats where the packs were settled, needing to maximize their home range size by using lower-quality patches to attain their resources (Morales-González et al. 2022), find mates, and find a suitable new territory.

Activity patterns between and among groups across seasons

In this study, we used four complementary measurements to understand when and how long wolves were active across seasons, and between non-residents and residents. Sarıkamış wolves were nocturnal across the seasons, but the degree of nocturnality was higher year-round in non-resident wolves and for both groups in the nomadic season. Many previous studies have shown that wolves become more nocturnal when in close proximity to people (Theuerkauf et al. 2003, Kusak et al. 2005). Our study suggests that these changes in

Table 6. Time spent active in each part of the day by season and group. Twilight accounted for an average of 17% of each 24 h period, with day accounting for 41%, and night accounting for 42%. The mean is reported for each group with the 95% confidence intervals reported in parentheses.

	Twilight	Day	Night
Nomadic season	0.13 (0.13–0.13)	0.15(0.14–0.15)	0.73 (0.72–0.73)
Pup-Rearing season	0.21 (0.21–0.21)	0.31 (0.31–0.31)	0.48 (0.48–0.48)
Residents	0.17 (0.16–0.17)	0.19 (0.19–0.19)	0.64 (0.64–0.64)
Non-Residents	0.17 (0.17–0.18)	0.24 (0.24–0.23)	0.58 (0.58–0.59)
Residents (Nomadic)	0.13 (0.13–0.13)	0.16 (0.16–0.16)	0.71 (0.71–0.71)
Residents (Pup-Rearing)	0.21 (0.21–0.21)	0.32 (0.32–0.32)	0.47 (0.47–0.47)
Non-Residents (Nomadic)	0.12 (0.12–0.12)	0.11 (0.11–0.12)	0.76 (0.76–0.77)
Non-Residents (Pup-Rearing)	0.21 (0.21–0.21)	0.28 (0.28–0.28)	0.50 (0.50–0.51)

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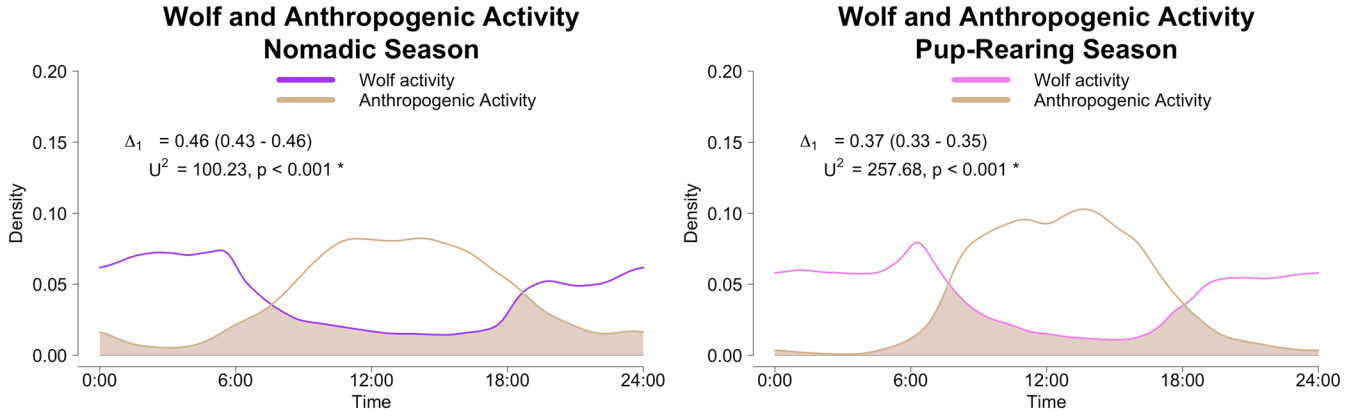


Figure 8. Diel activity distribution comparisons of wolves and people across seasons. Curves represent the smoothed kernel density distribution for each population. The shaded region represents the area under which both curves overlap. The estimated overlap coefficient and associated 95% confidence intervals are shown in the higher text, with the results of Watson's two-sample test of homogeneity shown below. Wolf activity was estimated using accelerometer data while human presence was estimated using camera traps.

activity may be sustained by the threat of humans even when they are not present in the forests. Alternatively, the threat of people, even when not present, may affect the activity patterns of prey species or intraguild competitors, so that wolves are reacting to these stimuli rather than directly to human presence (Theuerkauf and Rouys 2008, Bonnot et al. 2013).

In general, wolves were active for a significantly greater proportion of their day during the nomadic season than during the pup-rearing season (Fig. 5), with residents active for a greater proportion of their day than non-residents in the same season. This was not aligned with our original hypothesis that non-residents would be more active than resident wolves across all seasons. In fact, resident wolves were more active across both seasons, but this difference was not significant in the pup-rearing season. As we cannot account for human presence outside the forest, it is impossible to derive the exact driver of this difference. However, it is possible that human presence outside the forest does not differ as much as human presence inside the forest, allowing resident wolves to increase their activity while constraining non-residents. This hypothesis finds some support in our comparisons of human and wolf activity overlap between seasons.

The influence of people on a landscape can affect animals' activity patterns at both fine and coarse scales (Theuerkauf et al. 2003, Kusak et al. 2005, Nix et al. 2018, Suraci et al. 2021). We showed that human presence was low during the nomadic season, with all cameras in the array averaging less than one detection of human presence per day during this season compared to a three- to four-fold increase in the pup-rearing season (summer). While some animals are able to quickly adapt to changes in human abundance (Nix et al. 2018, Suraci et al. 2021), we showed that wolves had minimal changes in their activity patterns (93% overlap) between two seasons with substantially different amounts of human presence (Fig. 4). However, the overlap between wolf and human activity grew from 33% in the pup-rearing season to 47% in the nomadic season (Fig. 8). As humans are less present in the landscape at this time, this increase in overlap may be due to wolves willing to risk more overlap when human presence is lower in order to take advantage of some unknown rewards.

Conclusion

As wolf colonization continues in anthropogenically altered ecosystems, understanding how wolves interact with their environment is of paramount importance for wildlife managers. In the first GPS telemetry study on wolves in Türkiye, we documented the home range size and activity patterns of wolves in this area. We showed that even though human presence in the forest decreased, wolf home range sizes held constant. However, resident wolves did increase their activity overlap with people when people were less present in the landscape. This study offers one of the largest studies of seasonal changes in wolf home ranges and activity patterns in the densely populated regions of northwestern Asia. Furthermore, it adds to the growing understanding of how human presence may shape wolf behavior as they recolonize the more densely populated regions of Europe.

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Author contributions

J. David Blount: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead). **Austin M. Green**: Conceptualization (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Supervision (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Mark Chynoweth**: Data curation (equal); Formal analysis (equal); Investigation (equal); Writing – review and editing (equal). **Kyle D. Kittelberger**: Data curation (supporting); Investigation (supporting); Methodology (supporting); Resources (equal); Visualization (supporting); Writing – original draft (supporting). **Dário Hipólito**: Data curation (equal); Formal analysis (equal); Methodology (equal); Software (supporting); Writing – original draft (supporting). **Katarzyna Bojarska**: Conceptualization (supporting); Methodology (supporting); Validation (supporting); Writing – original draft (supporting). **Emrah Çoban**: Data curation (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Writing – original draft (supporting). **Josip Kusak**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing – original draft (supporting). **Çagan H. Şekercioğlu**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Writing – original draft (supporting).

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Data availability statement

GPS and activity data have been withheld from publication because of the vulnerable status of the study species. Output of home range size can be found in the Supporting information and all camera trap data have been deposited in Wildlife Insights: http://n2t.net/ark:/63614/w12003320 (Blount 2011).

Supporting information

The Supporting information associated with this article is available with the online version.

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