Remote Sensing in Ecology and Conservation
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RESEARCH ARTICLE

Cameras do not always take a full picture: wolf activity patterns revealed by accelerometers versus road-positioned camera traps

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Keywords
acceleration sensors, activity patterns, camera traps, *Canis lupus*, invasive methods, roads and trails, wildlife ecology

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Funding information
We are grateful to Fondation Segré and the Sigrid Rausing Trust for providing the majority of the funding for this project, and to other generous donors, including Arkadaşlar, Bilge Bahar, Seha İşmen, Ömer Külahçıoğlu, Burak Över, Batubay Özkan, Emin Özgür, Suna Reyent, Faruk Yalçın Zoo, National Geographic Society, STGM, TANAP, TÜBİTAK (under the 222 N122 Biodiversa+2021 call), Barbara Watkins, BTC Co., the Whitley Fund, Bernd Thies Foundation, UK Wolf Conservation Trust, EU LIFE Program, Croatian fund for Nature and Environment, and Plitvice Lakes National Park.

Editor: Dr. Marcus Rowcliffe
Associate Editor: Dr. Francesco Rovero

Received: 4 February 2025; Revised: 27 October 2025; Accepted: 4 November 2025

doi: 10.1002/rse2.70045

Abstract

While animal-attached devices provide the most detailed information on animal behaviour, camera traps have become an increasingly popular non-invasive alternative in wildlife ecology. Here, we compared activity patterns of wolves (*Canis lupus*) assessed with accelerometers and road-positioned camera traps in two study areas in Croatia and north-eastern Türkiye. We used accelerometer data from 37 wolves and camera trap data from 82,375 camera trap days at 358 road locations from 2010 to 2021. We fitted generalised additive mixed models to determine the times of day and parts of the year with the highest and lowest wolf activity and correlated the predictions between accelerometer- and camera-based models. Wolf activity patterns predicted from road-positioned camera traps and accelerometer data were significantly positively correlated, but the strength of the correlation varied among areas, times of day and seasons. The lowest and highest activity periods showed little overlap between the two methods. In both study areas, camera trap data failed to detect the increase in daylight activity during the pup-rearing season evident in accelerometer data. Overall, camera traps proved adequate for describing general daily and seasonal wolf activity patterns, while discrepancies between the two methods may largely be attributed to camera placement on roads. In light of the increasing use of camera traps in ecological research, our results highlight the value of animal-attached devices for tracking individuals and recommend caution when interpreting activity patterns from road-mounted cameras.

Introduction

Activity patterns are an essential part of animals' adaptations to their environment (Gilbert et al., 2023). The decision of when to be active is associated with the optimization of foraging, but also with varying exposure to risk and unfavourable environmental conditions (Owen-Smith, 1998; Suselbeek et al., 2014). Therefore, activity patterns have vital consequences for individual fitness (Downes, 2001; Werner & Anholt, 1993). Currently, animal-attached acceleration sensors offer the most precise technique of measuring activity, based on high-frequency measurements of changes in body movements in multiple directions (reviewed by Brown et al., 2013). However, this method of measuring activity requires tagging wild animals with devices, which is considered invasive, labour-intensive and expensive. These issues contribute to a wider debate about whether non-invasive methods can replace telemetry tracking in wildlife ecology studies (Zemanova, 2020).

Recently, camera traps have become an attractive alternative to estimate wildlife activity patterns (Bridges & Noss, 2011; Ridout & Linkie, 2009; Rowcliffe et al., 2014). Compared to animal-attached devices, camera traps allow less expensive data collection with minimal disturbance. However, the results obtained via camera trapping are strongly influenced by camera placement and species-specific behavioural and ecological traits (Cusack et al., 2015; Lashley et al., 2018). Placing cameras at random locations has been recommended to minimise this bias (Rowcliffe et al., 2014). Nevertheless, researchers frequently mount the cameras at sites that maximize encounters, especially in rare and elusive species, like large carnivores (Bubnicki et al., 2019; Iannino et al., 2025; Naderi et al., 2021). This may produce biased results, especially when the selection for roads depends on the type of activity and time of day or season. For instance, large carnivores in human-dominated landscapes use roads primarily for fast movement and mostly at times when the risk of encountering humans is the lowest, and they avoid them for sensitive behaviours, like resting (Bojarska et al., 2020; Bojarska et al., 2021; Zimmermann et al., 2014).

When different methods are used to investigate the same ecological question, it is crucial to test for differences and potential biases associated with each of them. With the growing popularity of camera traps, there is a need to validate whether the data obtained with this method, especially when cameras are not placed randomly, are comparable with other methods. So far, researchers have tried to compare the relative efficacy of camera traps and telemetry to estimate animal densities (Ivan et al., 2013; Sollmann et al., 2013), space use (Ferrer-Ferrando et al., 2023; Popescu et al., 2014), and activity patterns (Iannino et al., 2025; Lashley et al., 2018; Wolfson et al., 2023). The studies concluded that data collected by the cameras were relatively consistent with telemetry, which is largely due to the positive relationship between the likelihood of being recorded by a camera and the animal's movement rates (e.g. Luo et al., 2020). At the same time, studies have highlighted several issues regarding the design of camera trap studies, related to, for example, low consistency of camera-trap efficacy across ecological conditions (Lashley et al., 2018; Popescu et al., 2014). Therefore, there is an ongoing demand to validate camera traps in different systems and study designs as a tool for ecological studies.

In this study, we investigate the activity patterns of wolves (*Canis lupus*) obtained via acceleration sensors and road-positioned camera traps. Most of the studies on wolf activity have used VHF telemetry or GPS-telemetry travel speed and revealed bimodal patterns with twilight peaks or nocturnal patterns, which correlate with the proportion of domestic animals in their diet and levels of human disturbance (Ciucci et al., 1997; Kirilyuk et al., 2021; Theuerkauf, 2009). So far, only a few studies have used acceleration sensors to estimate wolf activity (Blount et al., 2024; Kirilyuk et al., 2021; Petroelje et al., 2020).

Our goals were (1) to describe circadian and seasonal wolf activity patterns recorded with the use of accelerometer and camera-trap data in Croatia and north-eastern Türkiye and (2) to test for differences in wolf activity patterns derived by the two methods. The two study areas differ fundamentally in ecological conditions that influence wolf behaviour, especially in the availability and use of natural and anthropogenic food sources and the level of habitat modification. Home ranges of wolves in Croatia consist mainly of forested areas, whereas in north-eastern Türkiye, they largely use open areas because the forest patches are sparse (authors' unpublished data). Although wolves in both areas feed on livestock, Croatian wolves prefer to feed on a diverse wild ungulate community, even in areas where their availability is low (Buzan et al., 2024; Octenjak et al., 2020). Livestock abundance and grazing pressure in Croatia are low, to the point that forest succession is a challenge for the conservation of grasslands and species depending on them (Ljubicic & Bilusic, 2022). On the contrary, wild ungulates in north-eastern Türkiye are rare except for the wild boar *Sus scrofa* (Kusak & Sekercioglu, 2021), and wolves rely mostly on abundant livestock and their carcasses and small mammals (Capitani et al., 2016). The abundance of livestock is at carrying capacity.

Due to temporary variable selection patterns in road use by wolves, we predicted that camera trap activity estimates would be higher than accelerometer-based activity estimates during periods of lowest human presence. We discuss the implications of camera use on roads for studying wildlife activity.

Materials and Methods

Study area

We conducted the study in the Dinaric Mountains of northern Croatia and the Kars province of north-eastern Türkiye.

Croatia

The study area consisted of two adjacent sites located 60 km apart: one in Gorski kotar and the other in the Lika region (Table S1, hereafter: Gorski kotar and Lika). The core study areas, where we collared the wolves and deployed the cameras, covered c. 800 km^2 in Gorski kotar (45.297°–45.673° N, 14.363°–14.8403° E) and 500 km^2 in Lika (44.561°–45.167° N, 14.937°–15.857° E). Some of the collared individuals roamed over larger areas, covering up to 1800 km^2 (45.297°–45.844° N, 14.221°–14.8403° E) in Gorski kotar and 3000 km^2 (44.561°–45.167° N, 14.937°–15.857° E) in Lika. The information on the landscape, climate and habitats is available in Supplementary file 1.

The wild ungulate community consists of wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and a few chamois (*Rupicapra rupicapra*) (Kusak & Krapinec, 2010). Three large carnivore species inhabit the area: brown bear (*Ursus arctos*), grey wolf and Eurasian lynx (*Lynx lynx*) (Jeremić et al., 2011). Cattle, goats, sheep and horses are grazed in Gorski kotar but are mostly concentrated along the coastal part of the region, outside of wolf home ranges (Jeremić et al., 2011). In Lika, sheep constitute most domestic animals, and preventive measures against wolf attacks are commonly implemented (Jeremić et al., 2011). Livestock constitutes 33% of the wolf diet in Gorski kotar and 63.5% in Lika, while wild ungulates form the remaining part (Octenjak et al., 2020). Wolves were strictly protected in Croatia except for 2005–2012, when legal shooting was introduced as part of wolf management. Despite this, wolves in Croatia are constantly under pressure from illegal killing (Kusak et al., 2019).

Türkiye

We conducted the study in the Kars province of north-eastern Türkiye (40.191°–40.455° N, 42.395°–42.758° E), a country where there are not enough protected areas and habitats and wildlife is under great pressure (Şekercioğlu et al., 2011). The core study area, where we trapped wolves and deployed the cameras, covered c. 600 km^2. Together with the surrounding areas used by wolves collared in this study, the extended study area covered c. 8000 km^2 (39.794°–40.679° N, 41.763°–43.377° E). The information on the landscape, climate and habitats is available in Supplementary file 1.

Thousands of cattle, sheep, and goats graze on pastures and inside the forest patches from April to November, following the availability of water and grass (Kusak & Sekercioglu, 2021). Livestock herds are accompanied by shepherds and dogs and kept in guarded pens overnight, but their carcasses are usually left for scavengers (Kusak & Sekercioglu, 2021). Among wild ungulates, only wild boar is abundant, while red deer is regionally extinct and roe deer is rare (Chynoweth et al., 2016; Naderi et al., 2021). Wolves, Caucasian lynx *Lynx lynx dinniki*, and brown bears inhabit the study area. Wolf diet in spring and summer consists mostly of livestock and small mammals (each of the categories forms c. 40% of the diet), while wild ungulates (wild boar) constitute a minor part (Capitani et al., 2016). The winter diet of wolves has not been studied in the area, but wolves have been frequently observed preying on domestic dogs in the villages (pers. obs). During the study, wolves were strictly protected in Türkiye, but illegal killing was an important mortality factor (Kusak et al., 2018).

Data collection

Camera trapping

We conducted the camera trapping from 2010 to 2021. During this time, we performed 1349 (Croatia: 1022, Türkiye: 327) camera trapping sessions lasting on average 67 days (Croatia: 56 ± 47, Türkiye: 77 ± 98), accounting for a total of 86,313 camera trap days (Croatia: 57,221, Türkiye: 29,092). We placed camera traps at forest roads and their intersections at 358 locations (Croatia: 202, Türkiye: 156). The number of cameras in different locations varied over the years, from 11 to 56 in Croatia and 4 to 51 in Türkiye. In Türkiye, the camera trapping was initially conducted from spring to autumn, and the winter season was included only during the last 3 years of the study. No data were collected in Türkiye in 2017 due to funding issues.

We selected camera-trap sites based on a grid (2 × 2 km in Türkiye, 2.5 × 2.5 km in Croatia). We chose the grid cells randomly and placed cameras at forest roads and their intersections within the selected cells. We did not use any bait or attractant at the camera trap stations. We used Reconyx (HPX2, PC900) and Keepguard

(891, 895, 571) cameras in Türkiye, and UVision (UV565 and UM595-3G) and Ltl Acorn in Croatia. Camera traps were set for continuous activity, five-picture series per trigger with no delay, auto or high sensitivity, and a 10-s sensor break between series. All cameras were set to record the date and local time. We replaced batteries and downloaded the photos approximately every 3 months.

Accelerometers

Wolves were captured and handled by permissions E-21264211-288.04-1602322 and 72784983-488.04-114100 (Türkiye's Department of Nature Conservation and National Parks and the Ministry of Agriculture and Forestry) and UP/1–612-07 /14–48/107, UP/1–612-07/15–48/47, UP/I-612-07 /17–48/75 and UP/I-612-07/19–48/76 (Croatia's Ministry of Environmental and Nature Protection, Ministry of Environmental Protection and Energy). We trapped wolves using rubber-padded leghold traps (LPC #7 EZ Grip, Livestock Protection Company, Alpine, Texas) and applied immobilisation and handling procedures according to an established protocol (Kusak et al., 2005). We fitted the captured wolves with GPS collars (Vectronic Aerospace GmbH, Berlin, Germany, models: GPS Pro, GPS Plus and Vertex) equipped with activity sensors (accelerometers). The sensors measured the acceleration in two or three (depending on the model) axes and indexed the differences in acceleration between consecutive measurements every 5 minutes. The raw data consisted of the average values of these differences, ranging from 0 to 255, recorded every 5 min for each axis. Because the acceleration measured in the third axis was only available for 7 (18%) individuals, we discarded the data from this axis and used the sum of raw values for the two axes to measure activity (from 0 to 510) (Bryce et al., 2022; Lorand et al., 2025; Petroelje et al., 2019).

We obtained accelerometer data from 37 individuals, 20 from Croatia (2003–2021) and 17 from Türkiye (2011–2021, Table S1). The data consisted of 2,914,125 activity records (measured every 5 min) corresponding to an average of 266 ± 179 days of monitoring per individual.

Statistical analyses

Wolf activity based on camera trap data

Using camera trap data, we analysed the patterns of wolf activity over time, i.e. different parts of the year and different hours of the day. We uploaded photos pictures from camera traps into Camelot (https://camelotproject.org/, in Croatia) or Wildlife Insights (https://www.wildlifeinsights.org/, in Türkiye) and manually identified them to the species level when possible. We obtained 228,853 and 261,737 photos of mammals (including humans) in Croatia and Türkiye, respectively. Of these, 2211 in Croatia and 1239 in Türkiye included wolves. We filtered wolf records by a minimum of 1-min intervals between the photos, which allowed us to eliminate photos taken within a series. We assumed that for activity analyses, the condition of true record independence may be relaxed (Peral et al., 2022), especially since we used non-linear splines to fit the effects of time of day and day of the year in the models (see below).

We estimated wolf activity distribution over time (both time of day and seasons), given time availability (Frey et al., 2017). We used 934 wolf occurrences (i.e. photos taken by camera traps) in Croatia and 316 in Türkiye (i.e. all available after applying a 1-min filter). Next, for each day within a camera-trap session, we generated one random data point (i.e. 57,221 random hours in Croatia and 29,092 random hours in Türkiye) with a random hour (ranging from 0 to 24). In the statistical models, we analysed wolf occurrences in relation to these random data points (as a measure of time availability) to identify the temporal peaks of wolf activity (see Frey et al., 2017).

We fitted generalized additive mixed models (GAMMs) using the 'mgcv' package (Wood, 2017) in R (R Core Team, 2021) separately for Croatia ($GAMM1_{CRO}$) and Türkiye ($GAMM1_{TUR}$). We used a binomial error distribution with a logit link and 'REML' as a smoothing parameter estimation method and wolf presence (1—wolf occurrence, 0—random data point) as a response variable. We used two continuous explanatory variables: day of year and hour of day. These two variables were fitted as the interaction of tensor product smooths (Wood, 2017), with the upper dimension of each smooth (parameter k) set to 10 (default). This means that the fit was allowed to vary between a straight line ($k = 1$) and complex curvature ($k = 10$). Using nonparametric smoothers implemented in GAMMs allows the modelling of non-linear associations between explanatory and response variables, and in this procedure, optimal fit is estimated directly from the data (i.e. does not have to be defined *a priori*; Wood, 2017). Using the interaction of tensor product smooths, we assumed that wolf activity in different parts of the day may depend on the season. We use a cyclic type of marginal basis because day 0 and day 365, as well as hour 0 and hour 24, are assumed to have the same level of wolf activity, so the only fits whose ends match should be considered in the model. In addition, we used camera trap site identity and year as two random effects in the models with the help of ridge penalty splines (Wood, 2017) to account for possible data dependency. We used the 'k.check' function to test whether the basis dimensions selected in tensor product smooths are appropriate and checked whether increasing 'k' parameter changes the general pattern of temporal wolf activity predicted by the model. Also, to evaluate the fits of the two models, we correlated observed wolf activity and activity predicted by the model. The results of $GAMM1_{CRO}$ and $GAMM1_{TUR}$ identified the times of day and parts of the year with relatively high and low wolf activity in the two countries, as found with the camera traps.

Wolf activity based on accelerometer data

Using accelerometer data, we analysed the patterns of wolf activity over time, that is, different parts of the year and different hours of the day. First, we reduced the original dataset of 2.8 million accelerometer records taken every 5 min by aggregating all the records into larger 30-min sections. For each such section, we calculated the mean hour of the day, mean day of the year, and mean wolf activity recorded by the activity sensor from six original records available. The resulting database consisted of 469,575 data records (220,794 in Croatia and 248,781 in Türkiye).

We fitted generalised additive mixed models in the 'mgcv' R library to explain wolf activity as assessed by accelerometer data in Croatia ($GAMM2_{CRO}$) and Türkiye ($GAMM2_{TUR}$). We used the day of the year and hour of the day as two continuous explanatory variables fitted with the interaction of cyclic tensor product smooths (procedure as in GAMM1). The distribution of the wolf activity index, as estimated by the accelerometers, was heavily right-skewed and contained a substantial proportion of zeros (16%), so we used the Tweedie family for error distribution with automatic p parameter optimisation and logarithmic link. We also fitted individual wolf identity and year as two random effects with the help of ridge penalty splines, to account for possible temporal dependency and individual features of certain individuals.

Comparing wolf activity based on camera trap and accelerometer data

To compare wolf activity based on camera trap data (models $GAMM1_{CRO}$ and $GAMM1_{TUR}$) and accelerometer data ($GAMM2_{CRO}$ and $GAMM2_{TUR}$), we correlated the predictions of these two sets of models. For this purpose, we created a matrix composed of days (ranging from 1 to 365, every 1 day) and hours (0–24, every 0.33 h) with 26,718 cells and calculated predicted values from the two sets of models for all 26,718 cells in the matrix (i.e. all the combinations of days and hours). Next, we correlated these predictions between camera-trap models and accelerometer-based models in two countries to assess similarities between wolf activity patterns obtained by the two methods. Moreover, we identified days of the year and hours of the day in which relative wolf activity is expected to be the highest (above the 90th percentile) and lowest (below the 10th percentile) in camera trap data, as compared to accelerometer data in both countries.

Finally, we compared the overlap of time windows of the lowest (≤10th percentile) and the highest (≥90th percentile) wolf activity, as predicted by models using camera traps and accelerometers. High overlap means that the camera traps and accelerometers identify the same part of the day and part of the year as the time window with the highest (or the lowest) wolf activity (i.e. the two methods identify similar wolf activity patterns). Since model similarity can also be obtained by chance, we also computed random overlap as a reference based on 500 simulations, indicating the expected similarity of two independent models.

Results

Wolf activity based on data obtained from road-positioned camera traps

Camera trap-based statistical models explaining wolf activity, which contained temporal predictors (i.e. day of year and hour of day), were substantially more informative compared to intercept-only models (ΔAIC >100 in both countries). Observed wolf activity and the activity predicted by the models were positively correlated ($P < 0.001$ in both countries), but correlation coefficients were rather low (Spearman rho = 0.16 for $GAMM1_{CRO}$ and 0.15 for $GAMM1_{TUR}$). Wolf activity recorded by camera traps showed a significant temporal pattern (models $GAMM1_{CRO}$ and $GAMM1_{TUR}$). In both Croatia ($P = 0.007$) and Türkiye ($P < 0.001$), interactions of day of year and hour of day were significant, clearly indicating periods of higher and lower wolf activity (Fig. 1).

Based on camera trap data, wolves were the least active during the middle of the day, but this midday drop in activity was less evident in Türkiye in winter. Wolves in Türkiye showed overall low activity at night at the end of winter (c. 50–100 day of the year, Figs. 1 and 4). The highest activity was recorded in the winter nights in Croatia and late summer twilight hours in Türkiye (Figs 1 and 4).

Wolf activity based on accelerometer data

Wolf activity recorded by accelerometers was significantly explained by the day of the year and time of day, and

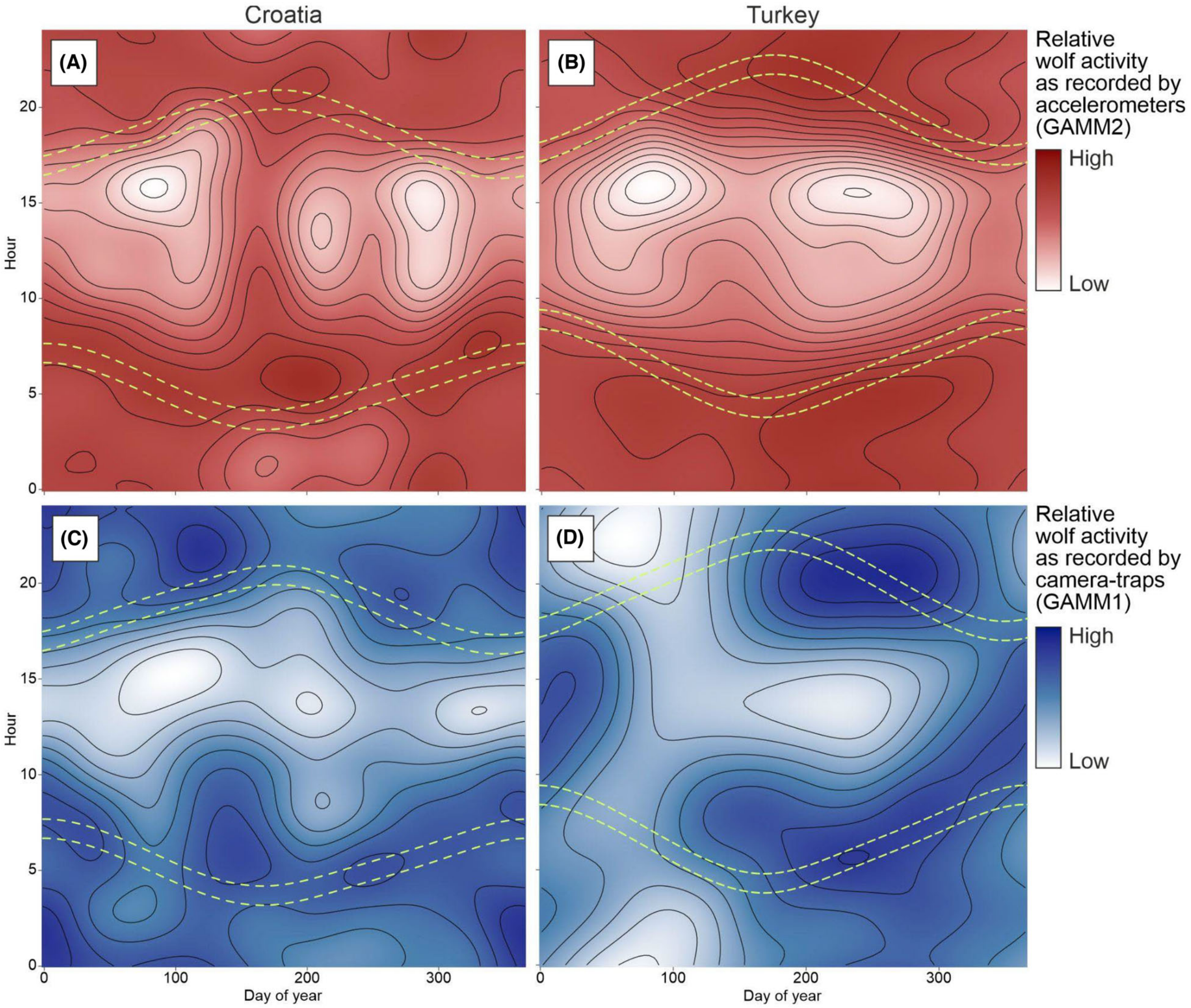

Figure 1. Wolf activity in Croatia and Türkiye in relation to the day of year and hour of day based on road-positioned camera trap data (C, D: models $GAMM1_{CRO}$ and $GAMM1_{TUR}$) and based on accelerometer data (A, B: models $GAMM2_{CRO}$ and $GAMM2_{TUR}$). Dashed lines indicate twilight periods (1 h before sunrise and 1 h after sunset); the day of year starts on 1 Jan; spring starts on day of year = 79, summer 172, autumn 265, winter 355.

including these two predictors in the models (as interacting splines) substantially reduced their AIC scores by >14,000 in both countries. Observed and predicted activities were strongly positively correlated ($P < 0.001$ in both models), and non-parametric correlation coefficients equaled 0.29 for $GAMM2_{CRO}$ and 0.40 for $GAMM2_{TUR}$. Wolf activity recorded by accelerometers showed clear temporal patterns, indicating periods with high and low activity (Fig. 1), and both day of the year and time of day were highly significant predictors of wolf activity in the two models (i.e. $P < 0.001$ in both $GAMM2_{CRO}$ and $GAMM2_{TUR}$).

Wolves in both study areas displayed the lowest activity levels during the mid-day-early afternoon period (Fig. 1). However, wolves retained relatively high activity levels throughout the day in late spring (between 150 and 180 days of the year, Fig. 1). The mid-day reduction of activity was also less evident in winter (Fig. 1). Wolves in Croatia increased their activity particularly in the early morning hours, but the timing of this peak (c. 5:00–7:00) remained constant irrespective of the season (Fig. 1), coinciding with daylight in summer. There was no apparent peak in wolf activity in the evening. Wolves in Türkiye retained elevated activity levels throughout the night. Their activity peaked during the summer nights (Fig. 1) when the period of increased activity also included dusk and dawn (Fig. 1).

Comparing wolf activity based on road-positioned camera traps and accelerometer data

Wolf activity patterns, as predicted by camera trap data and accelerometer data, were significantly positively correlated (Fig. 2). In Croatia, the correlation was stronger (Spearman $\rho = 0.73$, $P < 0.001$), while in Türkiye, it was substantially weaker but also highly significant ($\rho = 0.34$, $P < 0.001$).

In Croatia, the wolf activity levels recorded by camera traps were higher than accelerometer-based estimates during spring and autumn evenings and winter nights (Fig. 3). In Türkiye, camera trap data indicated generally higher activity levels during the day, especially in winter, and lower activity during the night. Additionally, camera-based estimates predicted lower overall activity in late spring in Türkiye. In both study areas, camera trap data did not register the increase in daylight and twilight activity in late spring that was recorded by the accelerometers (Fig. 4). The periods of lowest and highest wolf activity, determined by the two methods, rarely overlapped (Fig. 4).

The proportion of time window overlap between pairs of models ranged between 0.015 and 0.044 and was higher than random (i.e. 0.01), but also substantially below a complete overlap (i.e. 0.1, see Fig. S1). Time windows (i.e. part of the year and time of the day) of low wolf activity were relatively similar between camera trap-derived data and accelerometers in Croatia (overlap 0.044, see Fig. S1), while very different and close to random for high wolf activity in Croatia, with an overlap just c. 0.015 (Fig. S1).

Discussion

Wolf activity patterns derived by accelerometers and road-positioned camera traps are not equivalent, and the former exhibit a sharper and more evident pattern than the latter. We identified that general temporal patterns in wolf activity detectable in both camera trap data collected on roads and accelerometer data were consistent between the two countries. However, we also found substantial differences in the seasonal and daily patterns assessed by the two methods. We identified time windows when relative wolf activity was considerably different, as found by road-positioned camera traps compared to accelerometer data. Below, we discuss the possible drivers and practical implications of these differences between the two methods.

Wolf activity patterns revealed by accelerometers and camera traps

Based on the accelerometer data, we found a nocturnal rather than bimodal pattern in wolf activity in both areas. Elevated nocturnal activity in Croatian wolves is likely associated with a relatively high proportion of livestock in their diet, whereas high activity levels after sunrise during the denning period may be associated with increased movement rates, for example, returning to rendezvous sites after a hunt (Theuerkauf et al., 2003). In line with our predictions, wolves in Türkiye were more active during the night than the Croatian wolves. Wolves in our study in Türkiye must rely even more on live domestic animals and their carcasses, as they only occasionally feed on wild ungulates (Capitani et al., 2016).

The mid-day decrease in activity, detected both by accelerometer and camera-trap data, is probably associated with human avoidance, a typical strategy in many mammalian communities (Gaynor et al., 2018). However, wolves in both study areas retained relatively high activity throughout the day around May–June, coinciding with already high daily temperatures and rearing small pups. Bryce et al. (2022) found that wolves spent more energy during the pup-rearing period and increased their activity at night. We observed increased activity mostly during the day during this period in both study areas. During this time, pack cohesion decreases (Benson & Patterson, 2015), and individuals often hunt alone for juvenile ungulates (Gable et al., 2018) and smaller prey that is vulnerable also during the day, for example, small mammals (Capitani et al., 2016).

Comparison of the methods

The activity patterns predicted by road-positioned camera trap data were positively correlated with the accelerometer-based activity estimates, but the correlations were weak and lower in Türkiye than in Croatia. It shows that while generally activity patterns (i.e. time with relatively high or low wolf activity) obtained by the two methods were similar, substantial differences between the methods existed. We believe that some of the differences in activity patterns obtained with camera traps and accelerometers were related to the temporal variation in the behavioural responses of wolves to roads. In this study, higher camera trap activity estimates in the evenings in Croatia were probably a result of wolves using roads to travel to distant parts of their territories to search for prey (Theuerkauf et al., 2003). The camera traps failed to detect the change in activity in late spring, which coincided with the pup-rearing period, probably because most of this activity, associated

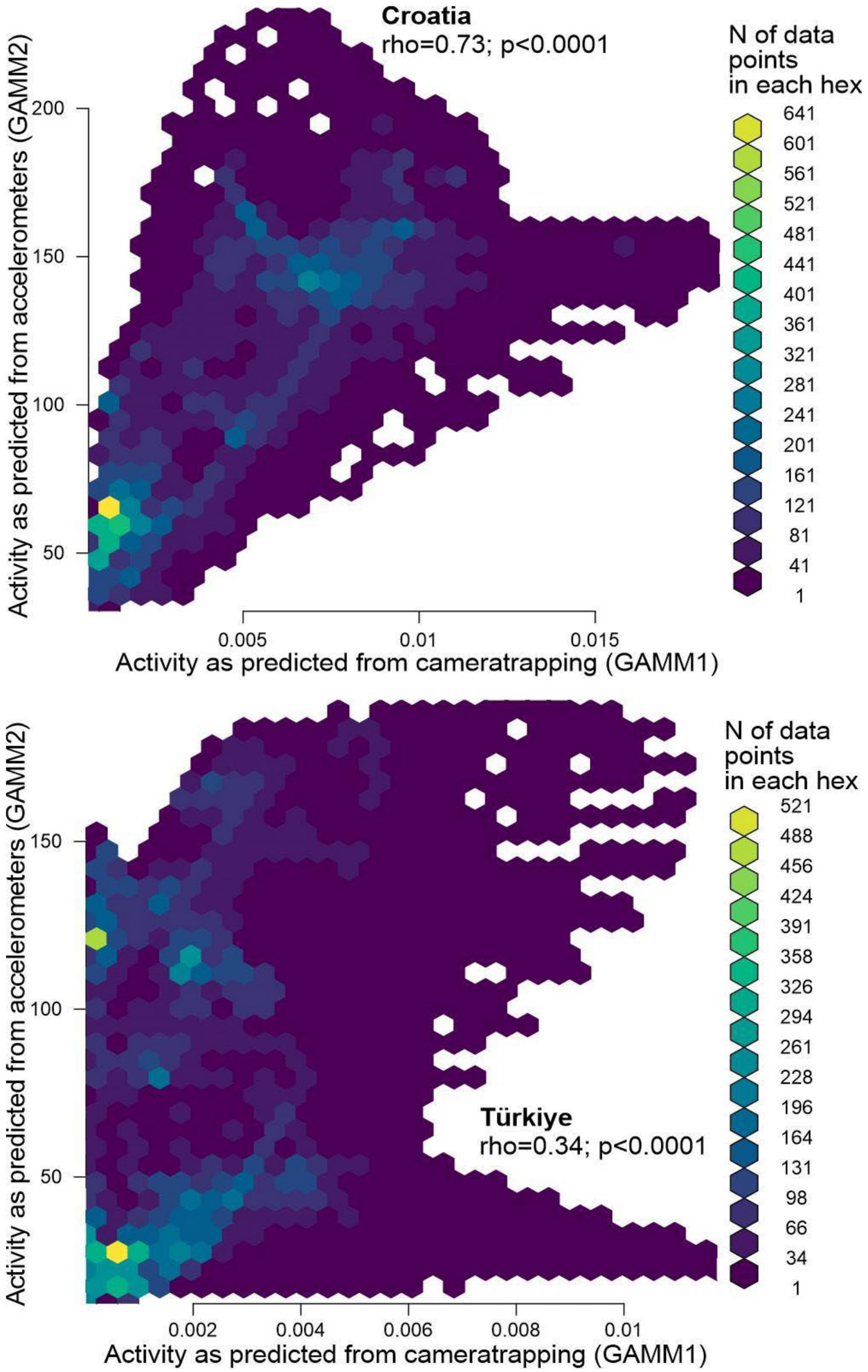

Figure 2. Correlation between temporal patterns of wolf activity based on accelerometer data (x-axis) and road-positioned camera trap data (y-axes) for Croatia (upper) and Türkiye (lower) for 26,718 data records of different times of day and days of year. Original datapoints are replaced with hexagonal bins, which are coloured based on the number of data points they contain.

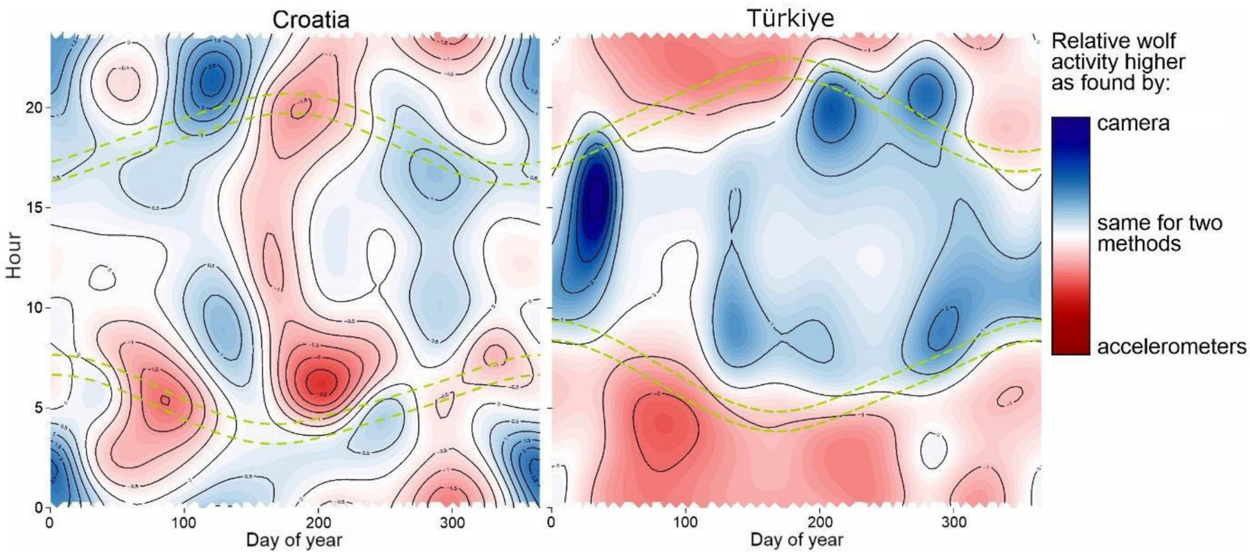

Figure 3. Differences between wolf activity based on road-positioned camera trapping (as predicted by GAMM1) and accelerometer data (GAMM2) in relation to the day of year and hour of the day in Croatia and Türkiye. The dashed lines indicate twilight periods (1 h before sunrise and 1 h after sunset). Interpretation of the day of year is given in Figure 1.

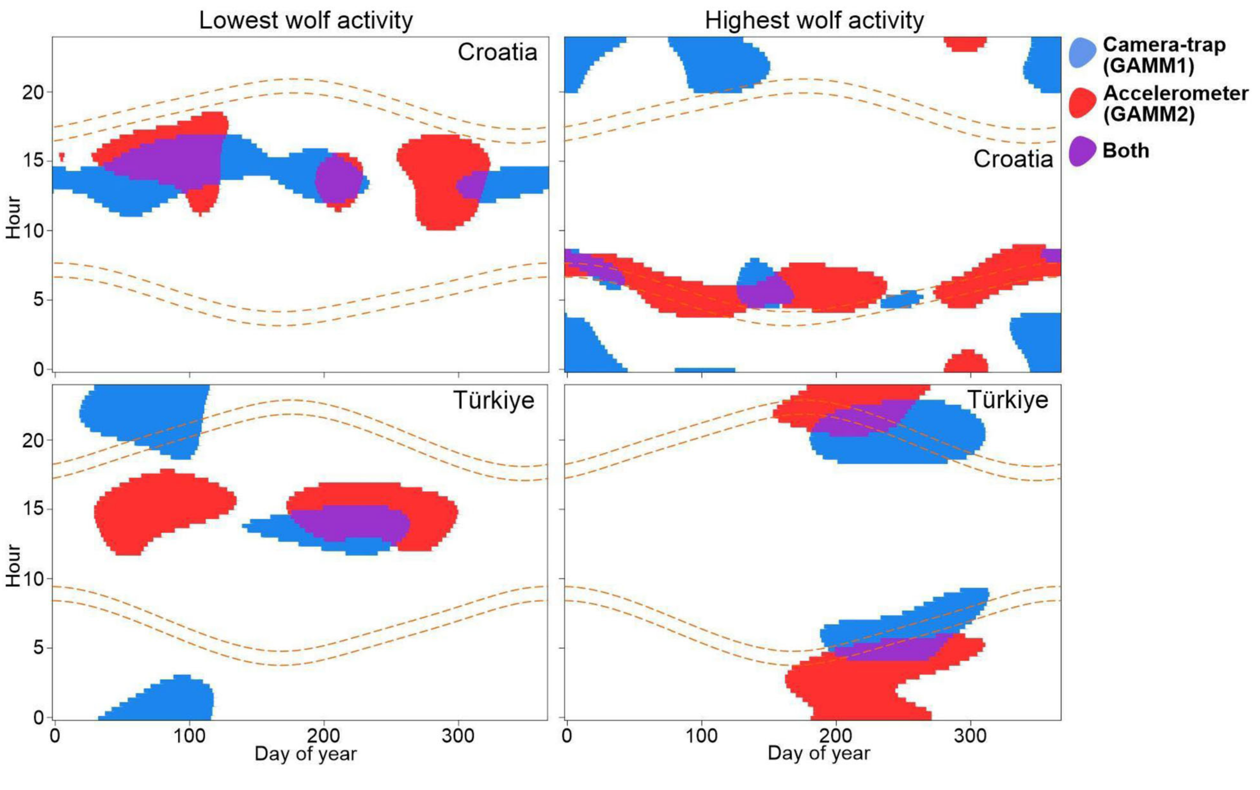

Figure 4. Time of the lowest (≤10th percentile) and the highest (≥90th percentile) wolf activity, as predicted by road-positioned camera trapping (GAMM1) and accelerometer data (GAMM2), and the overlap between the estimates obtained by the two methods, in Croatia and Türkiye. Interpretation of the day of year given in Figure 1.

with providing small prey to the breeding female and the pups, happened off roads.

High camera trap estimates on winter nights suggest that wolves in Croatia used roads more intensely during the snowy season. Some of the roads in the Croatian study areas are ploughed and/or used by vehicles, which may increase their selection by wolves (Droghini & Boutin, 2018). On the other hand, in the Turkish study area, people rarely use forest roads in the winter (Blount et al., 2024; Naderi et al., 2021), and at the end of the snowy season, there is often more snow on roads than off-road due to the sparser canopy cover, which probably prevented wolves from using them and caused overall low activity estimates around March.

Another potential source of the differences between accelerometer- and camera trap activity estimates may be related to the fact that camera traps were not distributed throughout the entire home ranges of all the individuals. Non-perfect spatial overlap between camera traps and animal-attached devices is often a source of divergent ecological estimates (Ivan et al., 2013; Popescu et al., 2014). Especially in wide-ranging species such as large carnivores, covering the whole home range with camera trapping is not always possible. This is particularly true when individuals use habitats where mounting camera traps is technically unfeasible due to a lack of trees and/or high theft risk, and especially when the use of such areas is not uniform across seasons and times of day. In this study, this was the case for wolves in Türkiye, which use some parts of their home ranges in non-forested areas (Blount et al., 2024).

We demonstrate that the assessment method impacts wolf activity pattern estimates. We found a stronger correlation between the predicted and observed wolf activity in accelerometer-based models than in camera-trap models, which indicates that temporal aspects capture a smaller part of the variation in wolf activity patterns obtained by road-positioned camera traps. We believe that the dissimilarity in camera trap- and accelerometer-derived activity patterns can be largely attributed to temporal patterns in wolf use of roads or habitats and areas where camera traps were not mounted. These aspects of wolf behaviour highlight some important limitations of camera trap studies. Detailed, telemetry-based spatiotemporal analyses are necessary to fully understand how wolf spatial behaviour affects the road-positioned camera trap capture rates (and therefore ecological estimates based on camera data). We recommend that future research addresses the potential bias related to camera placement by targeting more abundant species for which sufficient data can be obtained with randomly placed camera traps and including the type of activity in the analyses. Despite their high costs and invasiveness, GPS telemetry and animal-attached accelerometers remain indispensable tools in wildlife studies (Barber-Meyer, 2022; Merrill & Mech, 2003).

Acknowledgements

We thank the staff of Plitvice Lakes National Park, Risnjak National Park, Croatian Forests Ent, the staff and volunteers of the KuzeyDoğa Society and the residents of Erzurum, Kars and Sarıkamış for their dedicated support. We are grateful to H. Batubay Özkan and Barbara Watkins for their support of the Biodiversity and Conservation Ecology Lab at the University of Utah School of Biological Sciences. We thank Turkey's Department of Nature Conservation and National Parks and the Ministry of Agriculture and Forestry for granting the permits for this research. We are grateful to Fondation Segré and the Sigrid Rausing Trust for providing the majority of the funding for this project, and to other generous donors, including Arkadaşlar, Bilge Bahar, Seha İşmen, Ömer Külahçıoğlu, Burak Över, Batubay Özkan, Emin Özgür, Suna Reyent, Faruk Yalçın Zoo, National Geographic Society, STGM, TANAP, TÜBİTAK (under the 222 N122 Biodiversa+2021 call), Barbara Watkins, BTC Co., the Whitley Fund, Bernd Thies Foundation, UK Wolf Conservation Trust, EU LIFE Program and Croatian fund for Nature and Environment.

Author Contributions

Katarzyna Bojarska: Conceptualization; methodology; investigation; formal analysis; writing – original draft; writing – review and editing. **Michał Żmihorski:** Conceptualization; methodology; formal analysis; writing – original draft; writing – review and editing. **Morteza Naderi:** Investigation; writing – review and editing. **J. David Blount:** Investigation; writing – review and editing. **Mark Chynoweth:** Investigation. **Emrah Coban:** Investigation; project administration. **Çağan H. Şekercioğlu:** Investigation; funding acquisition; writing – review and editing; project administration. **Josip Kusak:** Investigation; project administration; writing – review and editing; funding acquisition.

Intellectual Contributions

Our study brings together authors from a number of different countries, including scientists based on the country where the study was carried out. All authors were engaged with the research and study design to ensure that the diverse sets of perspectives they represent were considered.

Data Availability Statement

The datasets and the code used in this study are provided in supplementary files. Raw data can be provided upon a reasonable request. Camera trap data from Turkiye are available at Blount, J. D. (2025). *Wildlife Insights*. Last Updated February 2025. Sarıkamış Camera Trapping Project. wildlifeinsights.org.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1 Supporting Information.