Community Ecology
https://doi.org/10.1007/s42974-024-00225-2

ORIGINAL ARTICLE

Camera trapping of forest mammals in Bükk Mountain, Hungary

Zsófia Szabó[1,2] · Péter Gombkötő[3] · Sándor Csaba Aranyi[4] · László Patkó[5] · Dóra Patkó[5] · Zoltán Barta[1]

Received: 22 July 2024 / Accepted: 4 November 2024

Abstract

The link between large- and middle-sized mammals in forest habitat is understudied in Central Europe; meanwhile these animals could have important effects on their habitats. In our study, we analysed camera trapping data obtained from May 2015 to September 2021 on 29 different sites in a temperate forest at the Bükk Mountain, Hungary. We investigated the temporal activity of ungulates (red deer, roe deer, wild boar) and predators (red fox and grey wolf), together with their response to human disturbance. We calculated temporal overlap value (Δ_4) and occurrence dynamics with multi-state modelling (msm). The results suggest that human activity was higher at daytime, while the mammals were more active at night. Multi-state modelling (msm) grouped animals and humans separately. Ungulates chose nighttime, when predators were also active, while they avoided daytime and human disturbance. Grey wolf were mostly co-occurred with its main food source, the red deer. Red fox overlapped the most with roe deer, suggesting that fox prey upon deer fawns. We found that human disturbance has a significant impact on the activity of forest mammals, whereas the expected avoidance of predators by ungulates does not appear to be evident. To better understand the effect of prey–predator behavioural responses in the presence of human disturbance, more field studies are needed in the region.

Keywords Human disturbance · Mammal · Predator · Prey · Ungulate · Interaction

Introduction

Europe's temperate ecosystems are complex, with their structure and function largely shaped by the presence and interactions of large (Putman, 1996; Kuijper et al., 2016) and medium-sized mammals (Stiegler et al., 2020). Ungulates, for instance, play a crucial role through seed dispersal, trampling, grazing, and browsing, which can alter habitats by opening spaces and modifying vegetation structure (Ramirez et al., 2018). This can lead to reduced densities for certain plant and animals species while favouring others (Carpio et al., 2021; Latham, 1999; Valente et al., 2020). Medium-sized carnivores, such as foxes and badgers (Tobajas et al., 2021), are key agents in removing carcasses (Goszczyński et al., 2000; Lazzeri et al., 2024; Young et al., 2015), and their burrowing behaviour can significantly influence soil conditions, hence promoting vegetation richness (Kurek et al., 2014), and even provide shelter (Kovács, 2007; Sidorovich et al., 2006) for breeding larger carnivores.

Apex predators, like grey wolves, exert a fine-tuning effect on these ecosystems through top-down regulation, primarily via direct predation (Jędrzejewski et al., 2002) and indirect mechanisms such as the "landscape of fear" effect (Laundre et al., 2010; Kuijper et al., 2013). These cascading effects can regulate prey populations and indirectly benefit vegetation (Kuijper et al., 2013) and other species (Dorresteijn et al., 2015; Mech, 2012).

Human presence is an increasingly significant component in these systems (Bengtsson et al., 2000), especially in a continent as densely populated as Europe. Continuous and growing human activity influences the temporal

✉ Zsófia Szabó
szabo.zsofia@science.unideb.hu

1 HUN-REN-DE Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, 1 Egyetem Tér, Debrecen 4032, Hungary

2 DE Juhász-Nagy Pál Doctoral School of Biology and Environmental Sciences, Debrecen 4032, Hungary

3 Directorate of Bükk National Park, 6 Sánc Utca, Eger 3304, Hungary

4 Division of Nuclear Medicine and Translational Imaging, Department of Medical Imaging, Faculty of Medicine, University of Debrecen, 98 Nagyerdei Körút., Debrecen 4032, Hungary

5 WWF Hungary, 69/a Álmos Vezér Útja, Budapest 1141, Hungary

Published online: 07 December 2024

behaviours of all of the above-mentioned species in ways that are not yet fully understood (Hebblewhite et al., 2005; Muhly et al., 2011; Preisser & Bolnick, 2008; Schmitz et al., 1997; Sih, 2005). Human presence in the temperate forests, whether through hunting, logging, (Ciuti et al., 2012; Theuerkauf & Rouys, 2008) jogging, or hiking, (Doherty et al., 2021) can alter animal movement, (Tucker et al., 2018) feeding habits (Ciucci et al., 2020), and predator–prey dynamics (Dorresteijn et al., 2015; Hebblewhite et al., 2005; Muhly et al., 2011; Sih, 2005).

In this exploratory study, we focused on one main questions: How does the presence of a large carnivore, specifically the grey wolf, affect the temporal distribution of its prey species in the presence of human disturbance in a temperate forest in Central Europe?

Study area

Our research was carried out in the central area of the Bükk Mountain, in the North Hungarian Mountains of the inner western Carpathians, in the Bükk National Park, northern Hungary (N 48°06′, E 20°30′). The study area has the largest continuous forest coverage (*c*. 140 km^2) in Hungary. This is one of the coldest parts of the country with mean annual temperature varying between 7–8 °C. The mean yearly rainfall is 600–700 mm (Baráz, 2002). Forest cover is 95% and formed by species like mountain and submountain beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and Austrian oak (*Quercus cerris*) (Baráz 2002; Juhász, 1959; Vojtkó, 1990). The main economic activity is forestry, managed by two large, state-owned companies (Egererdő Forestry Company and Északerdő Forestry Company). Many roads cross the study area, and it is a popular place for hunting, hiking and other recreational activities. Vehicular traffic consists of off-road vehicles, cars, trucks, tractors and motorcycles. Hikers mainly move on foot or ride on horse or bicycle. Seasonally, there are many mushroom collectors as well (P. Gombkötő pers. obs.). Hunting is a legal and popular recreational activity in the National Park.

The ungulate species in the area are red deer (*Cervus elaphus*, 10,085), wild boar (*Sus scrofa*, 2465), mouflon (*Ovis gmelinii*, 2332) and roe deer (*Capreolus capreolus*, 10,741). Main mesocarnivores are red fox (*Vulpes vulpes*), Eurasian badger (*Meles meles*) and European wildcat (*Felis silvestris*). Large carnivores besides grey wolf (*Canis lupus*) are Eurasian lynx (*Lynx lynx*) and occasionally brown bear (*Ursus arctos*) (Baráz 2002). Estimated game population numbers are based on the National Game Management Database (Csányi, 2022).

Methods

Camera traps

Use of camera traps is a non-invasive, cost-efficient method for wildlife monitoring (Kays & Keith, 2008). As it is a non-species specific approach, one can study more species simultaneously (Rowcliffe et al., 2008) and also investigate human disturbance. The frequency of animals captured on a camera trap correlates with their abundance and activity and thus can be a useful indicator of the occurrence of species in a given location (Carbone et al., 2001, 2002; Jennelle et al., 2002). Furthermore, camera traps are also suitable for studying the daily activity pattern of species in a habitat (Oliveira et al., 2017; Ridout & Linkie, 2009; Ross et al., 2013; Rossa et al., 2021).

We used RECONYX camera traps (UltraFire XR6; HyperFire HC500, PC900 and PC800; RapidFire PM75). Camera traps were installed on roads, trails, ungulate trails, mud baths where the presence of the wolf was previously confirmed by tracks and scats. The smallest distance between cameras was 240 m, and the largest was 8.81 km. The traps were inspected every 4 weeks to change batteries and memory cards. We analysed the data (both images and videos) obtained from the camera traps from May 2015 to September 2021 on 29 different sites.

The data

For each site, recordings were screened to collect the date and time of occurrences of studied species or human disturbance at a particular site. Following Ciuti et al. (2012), we categorised human disturbance into three types: hikers (including hunters), motorised vehicles (MV) and riders (cyclists and equestrians). The number of individual animals and humans was also recorded.

We analysed 135,540 files of 409.52 GB. We recorded 13,675 occurrences in total, of which were 747 *Canis lupus*, 1740 *Vulpes vulpes*, 2037 *Cervus elaphus*, 1752 *Sus scrofa*, and 1456 *Capreolus capreolus* observations. Furthermore, 4431 observations of human disturbance were recorded, including 1561 hikers and 2564 motorised vehicles. The remaining 1512 observations were excluded from the analyses because they involved mammals with fewer than 400 observations, such as riders, *Felis silvestris*, *Meles meles*, *Martes foina*, *Ovis gmelinii, Sciurus vulgaris, Lepus europaeus*, livestock, forestry and indeterminable observations, providing insufficient data for statistical evaluation.

To lower the level of pseudoreplication, we removed duplicate detection within 60 min except when we were sure that a different individual was present in the subsequent frames (Tobler et al. 2008).

All analyses were performed in the R environment (version 4.0.4, R Core Team, 2021).

Temporal overlap

We estimated temporal overlap coefficients (Δ_4: Weitzman 1970) between red deer, roe deer, wild boar, grey wolf, red fox, MV and hiker. Δ_4 ranges from 0 to 1, where 0 means no overlap, and 1 means complete overlap (Linkie & Ridout, 2011). Confidence intervals on Δ_4 values were computed after bootstrapping samples 100 times from the dataset. We performed this analysis with the "circular" and "overlap" R packages (Agostinelli & Lund, 2017; Linkie & Ridout, 2011).

For subsequent hierarchical clustering analysis (HCA), we used the $1–\Delta_4$ values of all species as the distance matrix. Clustering was based on the "Ward.D2" distance metric in R (Murtagh & Legendre, 2014). The optimal number of groups were estimated using the elbow method.

Multi-state modelling

To characterise the temporal co-dynamics of the studied species, we used a multi-state modelling approach. We consider that the surroundings of a camera trap can be in different states, namely individuals of what species (including human activities) occur there. This state is occasionally sampled by the given camera trap when it records a specimen; our data consist of a series of species identities and their recording time. We grouped these recordings for each continuous recording session at each site. These data groups serve as "subjects" in our analyses. We fitted a continuous time multi-state Markov model to these data by the "msm" R package (ver. 1.7.1, Jackson, 2011). As results we obtained, (i) the mean sojourn time, which is the average time a site spends in a given state and (ii) the matrix of probabilities that each state is next. One may interpret the sojourn times as the average time a species spends in the vicinity of the camera traps. On the other hand, the probabilities of next states indicate the frequency a species follows another species at the vicinity of camera traps. High probabilities mean that two species may co-occur together, while low probabilities indicate that species avoid each other. Because of convergence problems, we lumped the categories of "hiker" and "rider" under the name of "hiker" for this analysis.

Results

Temporal overlap

Predators and ungulates were mainly active during the night, while human activity peaked at the middle of the day (Fig. 1).

The Δ_4 values between human and ungulate activities were lower than values between wolf and ungulates. In the case of ungulates-human overlaps, we found the greatest Δ_4 value for roe deer ($\Delta_4 = 0.55$), followed by red deer ($\Delta_4 = 0.42$) and finally the wild boar ($\Delta_4 = 0.24$). The fox and wolf had an overlap value with human activity ($\Delta_4 = 0.38$ and $\Delta_4 = 0.42$) which is comparable to the overlap values between humans and ungulates. Regarding wolves and ungulates, the greatest overlap value was for red deer ($\Delta_4 = 0.90$) followed by roe deer ($\Delta_4 = 0.84$) and wild boar ($\Delta_4 = 0.81$). These indicate that the overlaps between wolf and ungulates were significantly higher than between human activity and ungulates. In the case of red fox, the smallest overlap value is with roe deer ($\Delta_4 = 0.76$). (Table 1.)

The HCA revealed three main groups with human disturbance factors clustered tightly together, fox and wild boar having similar temporal patterns, and red deer and roe deer share the most temporal overlap with grey wolf (Fig. 2).

Multi-state modelling

The Markov model indicated that the species spent relatively short time in the vicinity of camera traps (Fig. 3a). Red fox and grey wolf stayed the longest, while the ungulates and humans left quickly. According to the probabilities of the next state (Fig. 3b), human activities were strongly bounded, and they followed each other frequently. Human activities were less commonly followed by the animals. Within the animal species there is a strong bond between the ungulates, and a weaker one between the predators. Note, however, that predators are also connected to the red deer. Accordingly, human activities are closely placed in the transition diagram (Fig. 3c), and the other group is formed by the ungulates with rather strong links to predators. Animals are clearly avoided human activities.

Discussion

In our study area, the ungulates and predators are mainly active at night and dawn, while human activity can predominantly be observed at daytime and peaks at noon. As our observations are mainly taken from areas with human disturbance, these temporal characteristics of species occurrences

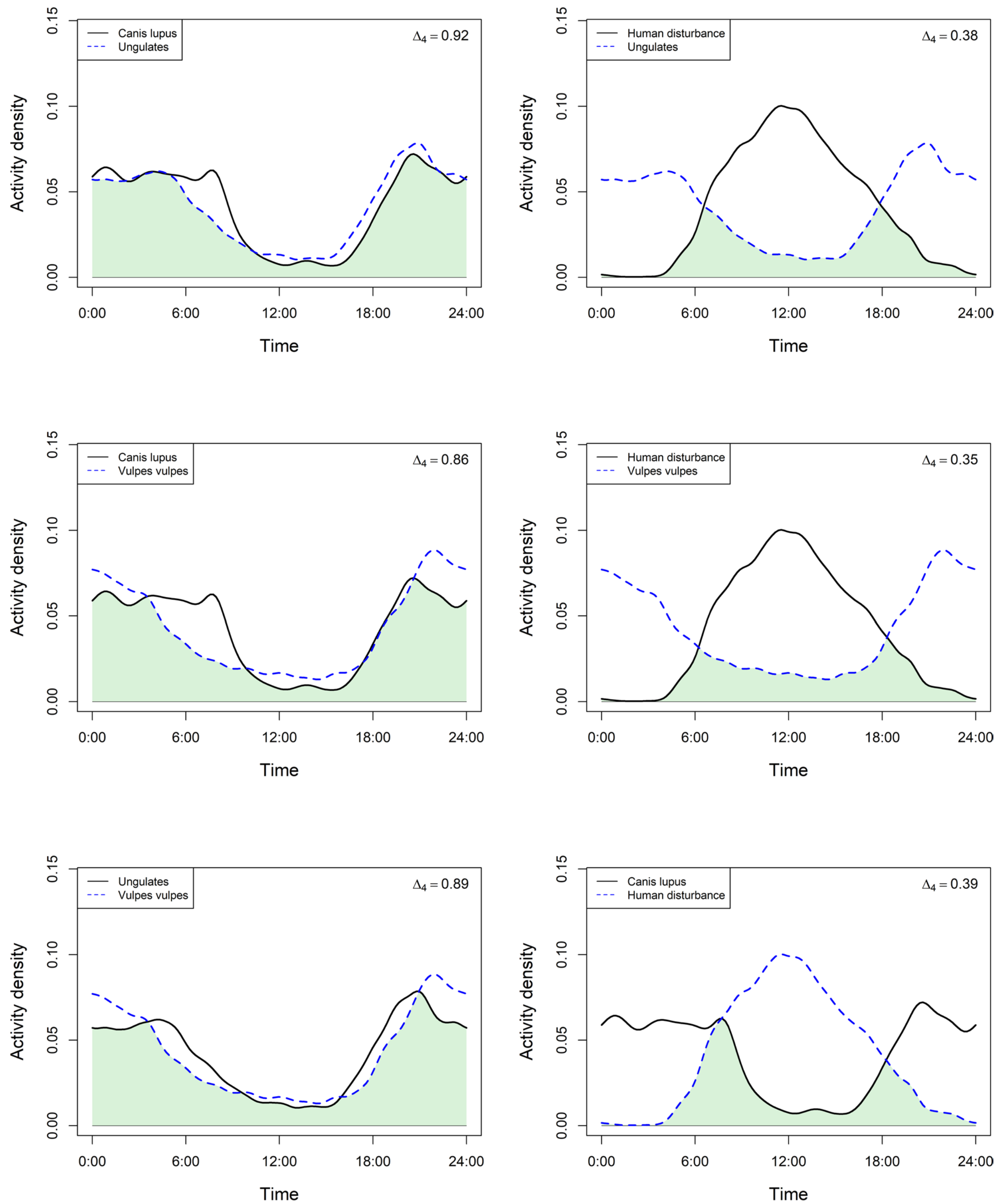

Fig. 1 Temporal overlap between human activity, grey wolf, red fox and ungulates (red deer, roe deer, and wild boar), between human activity and wolf, fox, and between predators (grey wolf and red fox) for all areas, in Bükk Mountain, Hungary, 2015–2021. The estimated overlap values (Δ_4) between two activity patterns range from 0 to 1, where 0 means no overlap, and 1 means complete overlap

may indicate previously reported effects. Human activity can modify the activity patterns of both predators and ungulates: the transition of diurnal animals to nocturnal life caused by human activity is a well-known, globally observed phenomenon (Frid & Dill, 2002; Gaynor et al., 2018). Also, human disturbance can change the predator's activity patterns indirectly through the changes caused in activity patterns of ungulates (Theuerkauf et al., 2003). Ungulates can adapt to predators and human disturbance by limiting their temporal or spatial overlap in their activities. According to previous observations, ungulates often change their daily activity pattern if a predator appears in the same habitat (Eccard et al.,

Table 1 Summary of overlap coefficients (Δ_4, for all sites), and their 95% confidence intervals (95% CI)

Overlap [95% CI]	MV	Hiker	*Cervus elaphus*	*Capreolus capreolus*	*Sus scrofa*	*Vulpes vulpes*
Hiker	0.78 [0.75; 0.80]	–	–	–	–	–
Cervus elaphus	0.42 [0.40; 0.44]	0.34 [0.32; 0.37]	–	–	–	–
Capreolus capreolus	0.55 [0.52; 0.58]	0.44 [0.41; 0.47]	0.85 [0.82; 0.88]	–	–	–
Sus scrofa	0.24 [0.22; 0.26]	0.18 [0.16; 0.20]	0.82 [0.79; 0.84]	0.66 [0.63; 0.69]	–	–
Vulpes vulpes	0.38 [0.35; 0.40]	0.31 [0.29; 0.34]	0.87 [0.85; 0.90]	0.76 [0.73; 0.79]	0.87 [0.85; 0.90]	–
Canis lupus	0.42 [0.39; 0.45]	0.32 [0.28; 0.35]	0.9 [0.87; 0.93]	0.84 [0.80; 0.88]	0.81 [0.77; 0.85]	0.85 [0.82; 0.89]

MV Motorised vehicles

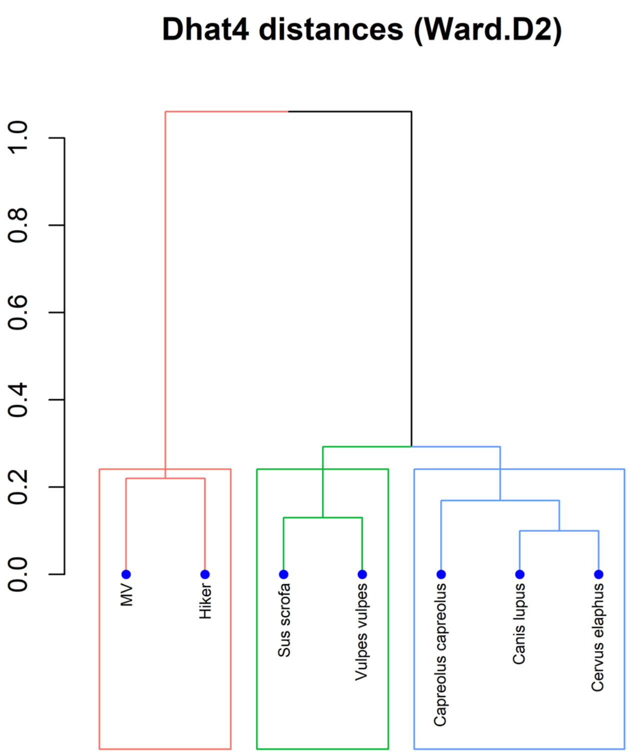

Fig. 2 Hierarchical clustering analysis of overlap coefficients (Δ_4) using the Ward.D2 distance metric. Optimal number of clusters were defined with the elbow method. MV, motorised vehicles

2008; Fenn & Macdonald, 1995; Gliwicz and Dąbrowski 2008; Mills & Shenk, 1992; Prat-Guitart et al., 2020; Ross et al., 2013).

Meanwhile, we could not detect the significant effect of the wolf presence. Our observation aligns with the results of Theuerkauf and Rouys (2008), where they found that ungulates did not avoid the areas used by wolves. Predators, however, are also able to adjust their activities to match those of the ungulates (Ross et al., 2013; Theuerkauf et al., 2003). Wolves had the highest overlap value with red deer, and detectable connection in msm analysis, which supports the results of Lanszki et al. (2012), as red deer is the main prey of wolves in Hungary.

Fox had the highest temporal overlap with roe deer, as its fawn's main predator (Jarnemo, 2002; Jarnemo & Liberg, 2005). Although anthropogenic food sources could be an important factor for foxes (Ciucci et al., 2020), they do not show a notable overlap with human disturbance. Instead, foxes exhibit the second-highest co-occurrence with wolves and red deer. Wolf kills of red deer could be a very important food source for foxes (Lazzeri et al., 2024).

Our result suggests that ungulates group together. With having a niche overlap, they use similar food sources but in different proportions and their browsing strategies can also differ (Latham, 1999; Spitzer et al., 2020). Wild boar was the most sensitive to both human disturbance and predators. The study of Theuerkauf and Rouys (2008) found that wild boar avoids main roads, while red and roe deer do not. Although predators could avoid human disturbance more (Dorresteijn et al., 2015; Theuerkauf & Rouys, 2008), in our msm results, they are positioned between human disturbance and preys. They may like to utilise dirt roads for travelling and avoiding human disturbance at the same time (Zimmermann et al., 2014).

Earlier studies suggest that grey wolf can have an important role in the ecosystem as a top predator. For example, the study of Kuijper et al. (2013) indicates that wolves can change the spatial patterns of ungulates browsing, and this can foster the regeneration of trees in a European forest. The top-down cascading effect caused by wolves is studied widely (Beyer et al., 2007; Gable et al., 2020; Hebblewhite et al., 2005; Kuijper et al., 2016; Ripple & Beschta, 2006, 2012; Ripple et al., 2014); however, there is no consensus about the significance of direct and indirect effects of wolves on prey and habitat (Kuijper et al., 2016; Marshall et al., 2013; Mech, 2012; Mech & Peterson, 2003; Middleton et al., 2013).

Grey wolves presence can pose additional direct or indirect predation pressure on the ungulates. Similarly to Visscher et al. (2023), our results suggest that this pressure, in comparison with strong human disturbance, is relatively mild for these species from a spatial and temporal perspective. Nevertheless, other studies have showed that predator presence may facilitate the increase in the local biodiversity,

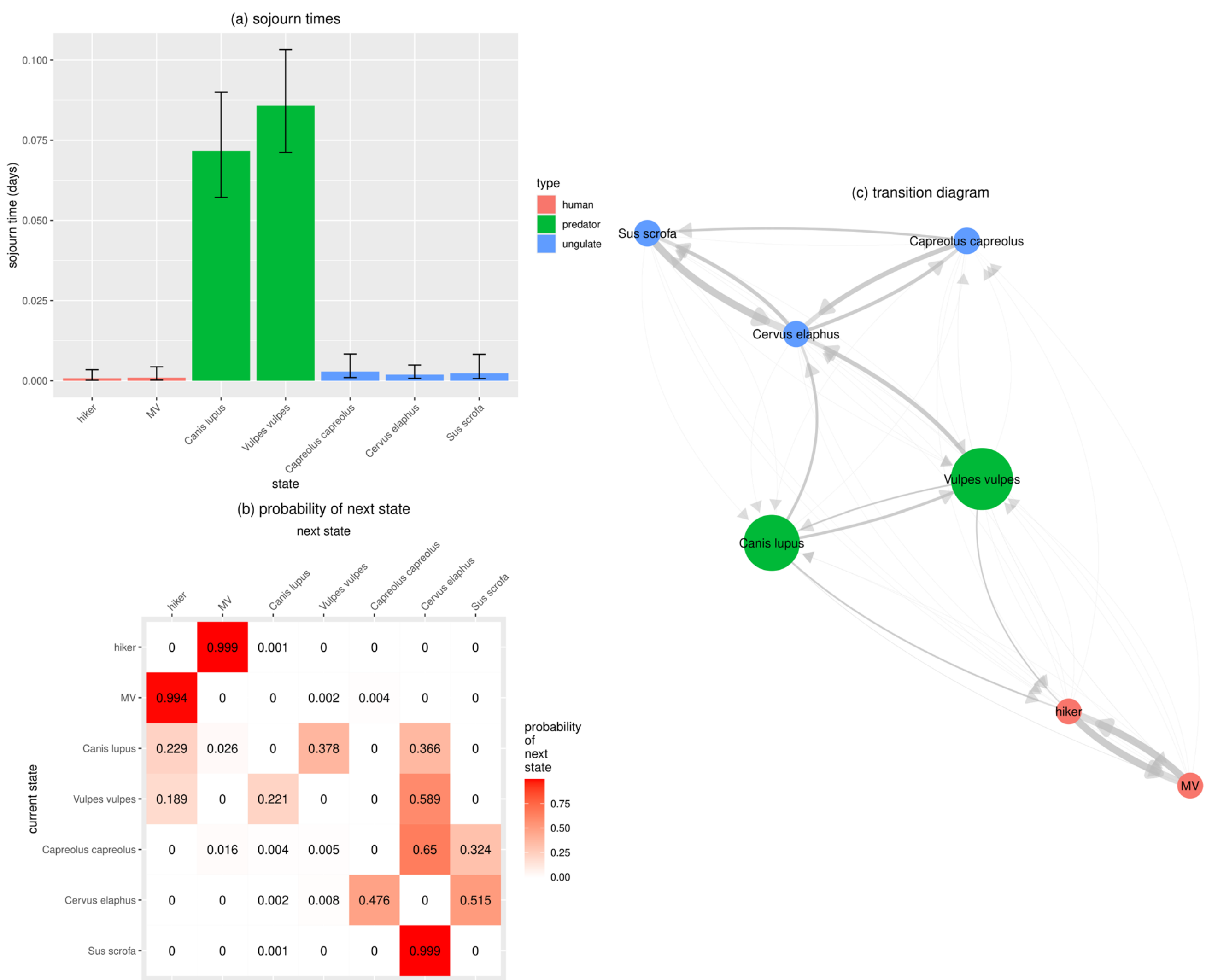

Fig. 3 Continuous time multi-state Markov analysis. **a** The mean sojourn time (with 95% confidence intervals) gives the amount of time species (including human activities) spend near camera traps. **b** The probabilities of next states characterise how frequently a species follows another one. **c** The transition diagram illustrates the relationships between species and human activities according to their tendency to follow each other (on the basis of probabilities of next state). The size of nodes is proportional to the sojourn times of the species. The arrows show who follows whom, while the line width indicates the transition probabilities. MV, motorised vehicles

for instance, by regulating the overabundant ungulate populations which has negative effect on the vegetation and biodiversity or by influence the behaviour and habitat use of the prey (Beyer et al., 2007; Dorresteijn et al., 2015; Hebblewhite et al., 2005; Kuijper et al., 2013, 2016; Ripple & Beschta, 2006, 2012).

In our study, we could not detect avoidant response from ungulates to predators in time, although they reacted to human disturbance. Ungulates grouped together, probably because of their niche and diet overlap. Wild boar avoided the most both predators and human disturbance. They may avoid roads, while deer and predators do not. In case of predators, wolves had the highest temporal overlap value with red deer, and strongest connection in msm analysis, as their main predator. Red fox also had strong connection with wolf and red deer, meanwhile showed the highest overlap with roe deer. Fox is the main predator of roe deer fawns, and red deer kills of wolves could be an important food resource, too.

Large- and middle-sized mammals have important roles in forest ecosystem. In our paper, we could investigate the connections between these mammals; however, their effect on the habitat was out of this study's scope and call for more research on this field.

Funding Open access funding provided by University of Debrecen. Nemzeti Kutatási, Fejlesztési és Innovációs Alap, TKP2021-NKTA-32, Zoltán Barta.

References

Agostinelli C, Lund U (2017) *R package "circular": Circular Statistics* (version 0.4–93)

Baráz, C. (Ed). (2002). *A Bükki Nemzeti Park*. Hegyek, Erdők, Emberek: Eger.

Beyer, H. L., Merrill, E. H., Varley, N., & Boyce, M. S. (2007). Willow on yellowstone's northern range: Evidence for a trophic cascade? *Ecological Applications, 17*, 1563–1571. https://doi.org/10.1890/06-1254.1

Bengtsson, J., Nilsson, S. G., Franc, A., & Menozzi, P. (2000). Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management, 132*, 39–50. https://doi.org/10.1016/S0378-1127(00)00378-9

Carbone, C., Christie, S., Conforti, K., et al. (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation, 4*, 75–79. https://doi.org/10.1017/S1367943001001081

Carbone, C., Christie, S., Conforti, K., et al. (2002). The use of photographic rates to estimate densities of cryptic mammals: Response to Jennelle et al. *Animal Conservation, 5*, 121–123. https://doi.org/10.1017/S1367943002002172

Carpio, A. J., Apollonio, M., & Acevedo, P. (2021). Wild ungulate overabundance in Europe: Contexts, causes, monitoring and management recommendations. *Mam Rev, 51*, 95–108. https://doi.org/10.1111/mam.12221

Ciucci, P., Mancinelli, S., Boitani, L., et al. (2020). Anthropogenic food subsidies hinder the ecological role of wolves: Insights for conservation of apex predators in human-modified landscapes. *Global Ecology and Conservation, 21*, e00841.

Ciuti, S., Northrup, J. M., Muhly, T. B., et al. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape Of Fear. *PLoS ONE, 7*, e50611. https://doi.org/10.1371/journal.pone.0050611

Csányi, Országos Vadgazdálkodási Adattár [Official Game Management Harvesting Database] (2022) A 2020/2021. vadászati év vadgazdálkodási eredményei valamint a 2021. tavaszi vadállomány becslési adatok és vadgazdálkodási tervek, Vadgazdálkodási tájegységi összesítések. MATE, VTI, Vadbiológiai és Vadgazdálkodási Tanszék, Gödöllő. http://www.ova.info.hu/vgstat.html. Accessed 21 Jul 2022

Doherty, T. S., Hays, G. C., & Driscoll, D. A. (2021). Human disturbance causes widespread disruption of animal movement. *Nat Ecol Evol, 5*, 513–519. https://doi.org/10.1038/s41559-020-01380-1

Dorresteijn, I., Schultner, J., Nimmo, DG. (2015). Incorporating anthropogenic effects into trophic ecology: Predator - Prey interactions in a human-dominated landscape. Proceedings of the Royal Society B: Biological Sciences 282: https://doi.org/10.1098/rspb.2015.1602

Eccard, J. A., Pusenius, J., Sundell, J., et al. (2008). Foraging patterns of voles at heterogeneous avian and uniform mustelid predation risk. *Oecologia, 157*, 725–734. https://doi.org/10.1007/s00442-008-1100-4

Fenn, M. G. P., & Macdonald, D. W. (1995). Use of Middens by Red foxes: Risk Reverses Rhythms of Rats. *Journal of Mammalogy, 76*, 130–136. https://doi.org/10.2307/1382321

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Ecology and Society*. https://doi.org/10.5751/es-00404-060111

Gable, T. D., Johnson-Bice, S. M., Homkes, A. T., et al. (2020). Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers. *Science Advances, 6*, eabc5439. https://doi.org/10.1126/sciadv.abc5439

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science, 360*, 1232–1235. https://doi.org/10.1017/S1473550416000240

Gliwicz, J., & Dabrowski, M. J. (2008). Ecological factors affecting the diel activity of voles in a multi-species community. *Annales Zoologici Fennici, 45*, 242–247. https://doi.org/10.5735/086.045.0401

Goszczyński, J., Jedrzejewska, B., & Jedrzejewski, W. (2000). Diet composition of badgers (*Meles meles*) in a pristine forest and rural habitats of Poland compared to other European populations. *Journal of Zoology, 250*, 495–505. https://doi.org/10.1111/j.1469-7998.2000.tb00792.x

Hebblewhite, M., White, C. A., Mckenzie, J. A. (2005). Human Activity Mediates a Trophic Cascade Caused by Wolves. *Biological Sciences Faculty Publications, 288*. https://doi.org/10.1890/04-1269

Jackson, C. (2011). Multi-State Models for Panel Data: The msm Package for R. Journal of Statistical Software 38:1–28. https://doi.org/10.18637/jss.v038.i08

Jarnemo, A. (2002). Roe deer Capreolus capreolus fawns and mowing—mortality rates and countermeasures. *Wildlife Biology, 8*, 211–218. https://doi.org/10.2981/wlb.2002.035

Jarnemo, A., & Liberg, O. (2005). Red fox removal and roe deer fawn survival—a 14-year study. *The Journal of Wildlife Management, 69*, 1090–1098. https://doi.org/10.2193/0022-541X(2005)069[1090:RFRARD]2.0.CO;2

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., et al. (2002). Kill Rates and Predation by Wolves on Ungulate Populations in Białowieża Primeval Forest (Poland). *Ecology, 83*, 341–1356. https://doi.org/10.2307/3071948

Jennelle, C. S., Runge, M. C., & MacKenzie, D. I. (2002). The use of photographic rates to estimate densities of tigers and other cryptic mammals: A comment on misleading conclusions. *Animal Conservation, 5*, 119–120. https://doi.org/10.1017/S1367943002002160

Juhász, L. (1959). A Bükki Nagymező növényzete. In: Acta Academiae Paedagogicae Agriensis, 5, 495–505, Dr Némedi Lajos, Eger

Kays, R. W., & Keith, S. M. (2008). Remote cameras. *Noninvasive survey methods for carnivores* (pp. 110–128). Island Press.

Kovács, Z. (2007) Farkasok a Kárpát-medencében. Corvina Kiadó Kft, Budapest

Kuijper, D. P. J., De Kleine, C., Churski, M., et al. (2013). Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography, 36*, 1263–1275. https://doi.org/10.1111/j.1600-0587.2013.00266.x

Kuijper, D. P. J., Sahlén, E., Elmhagen, B., et al. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic

landscapes. *Proceedings of the Royal Society B, 283*, 20161625. https://doi.org/10.1098/rspb.2016.1625
Kurek, P., Kapusta, P., & Holeksa, J. (2014). Burrowing by badgers (*Meles meles*) and foxes (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest. *Ecological Research, 29*, 1–11. https://doi.org/10.1007/s11284-013-1094-1
Lanszki, J., Márkus, M., Újváry, D., et al. (2012). Diet of wolves Canis lupus returning to Hungary. *Acta Theriologica, 57*, 189–193. https://doi.org/10.1007/s13364-011-0063-8
Latham, J. (1999). Interspecific interactions of ungulates in European forests: An overview. *Forest Ecology and Management, 120*, 13–21. https://doi.org/10.1016/S0378-1127(98)00539-8
Laundre, J., Hernández, L., & Ripple, W. (2010). The landscape of fear: Ecological implications of being afraid. *The Open Ecology Journal, 3*, 1–7. https://doi.org/10.2174/1874213001003030001
Lazzeri, L., Ferretti, F., Churski, M., et al. (2024). Spatio-temporal interactions between the red fox and the wolf in two contrasting European landscapes. *Science and Reports, 14*, 221. https://doi.org/10.1038/s41598-023-50447-z
Linkie, M., & Ridout, M. S. (2011). Assessing tiger-prey interactions in Sumatran rainforests. *Journal of Zoology, 284*, 224–229. https://doi.org/10.1111/j.1469-7998.2011.00801.x
Marshall, K. N., Hobbs, N. T., & Cooper, D. J. (2013). Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. *Proceedings of the Royal Society B, 280*, 20122977. https://doi.org/10.1098/rspb.2012.2977
Mech, L. D. (2012). Is science in danger of sanctifying the wolf? *Biological Conservation, 150*, 143–149. https://doi.org/10.1016/j.biocon.2012.03.003
Mech, L. D., & Peterson, R. O. (2003). Wolf-Prey Relations. *Wolves: behavior, ecology, and conservation* (pp. 131–160). University of Chicago Press.
Middleton, A. D., Kauffman, M. J., McWhirter, D. E., et al. (2013). Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters, 16*, 1023–1030. https://doi.org/10.1111/ele.12133
Mills, M. G. L., & Shenk, T. M. (1992). Predator-prey relationships: The impact of lion predation on wildebeest and zebra populations. *The Journal of Animal Ecology, 61*, 693. https://doi.org/10.2307/5624
Muhly, T. B., Semeniuk, C., Massolo, A., et al. (2011). Human activity helps prey win the predator-prey space race. *PLoS ONE, 6*, 1–8. https://doi.org/10.1371/journal.pone.0017050
Murtagh, F., & Legendre, P. (2014). Ward's hierarchical agglomerative clustering method: Which algorithms implement ward's criterion? *Journal of Classification, 31*, 274–295. https://doi.org/10.1007/s00357-014-9161-z
Oliveira, T., Chiriac, S., Corradini, A., Marcon, A. (2017). Factors influencing wolf (Canis lupus) detection rate in a camera trapping survey in the Eastern Carpathians, Romania. In: 10th Baltic Theriological Conference. pp 2–5
Prat-Guitart, M., Onorato, D. P., Hines, J. E., & Oli, M. K. (2020). Spatiotemporal pattern of interactions between an apex predator and sympatric species. *Journal of Mammalogy, 101*, 1279–1288. https://doi.org/10.1093/jmammal/gyaa071
Preisser, E. L., & Bolnick, D. I. (2008). The many faces of fear: Comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS ONE, 3*, 5–8. https://doi.org/10.1371/journal.pone.0002465
Putman, R. J. (1996). Ungulates in temperate forest ecosystems: Perspectives and recommendations for future research. *Forest Ecology and Management, 88*, 205–214. https://doi.org/10.1016/S0378-1127(96)03878-9
Ramirez, J. I., Jansen, P. A., & Poorter, L. (2018). Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: A semi-quantitative review. *Forest Ecology and Management, 424*, 406–419. https://doi.org/10.1016/j.foreco.2018.05.016
Ridout, M., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics, 14*, 322–337.
Ripple, W. J., & Beschta, R. L. (2006). Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management, 230*, 96–106. https://doi.org/10.1016/j.foreco.2006.04.023
Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation, 145*, 205–213. https://doi.org/10.1016/j.biocon.2011.11.005
Ripple, W. J., Estes, J. A., Beschta, R. L., et al. (2014). Status and ecological effects of the world's largest carnivores. *Science, 343*, 1241484. https://doi.org/10.1126/science.1241484
Ross, J., Hearn, A. J., Johnson, P. J., & Macdonald, D. W. (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. *Journal of Zoology, 290*, 96–106. https://doi.org/10.1111/jzo.12018
Rossa, M., Lovari, S., & Ferretti, F. (2021). Spatiotemporal patterns of wolf, mesocarnivores and prey in a Mediterranean area. *Behavioral Ecology and Sociobiology*. https://doi.org/10.1007/s00265-020-02956-4
Rowcliffe, J. M., Field, J., Turvey, S. T., & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology, 45*, 1228–1236. https://doi.org/10.1111/j.1365-2664.2008.01473.x
R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Schmitz, O. J., Beckerman, A. P., & Brien, K. M. O. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology, 78*, 1388–1399.
Sidorovich, V. E., Sidorovich, A. A., & Izotova, I. V. (2006). Variations in the diet and population density of the red fox *Vulpes vulpes* in the mixed woodlands of northern Belarus. *Mammalian Biology, 71*, 74–89. https://doi.org/10.1016/j.mambio.2005.12.001
Sih, A. (2005). Predator-prey space use as an emergent outcome of a behavioral response race. *Ecology of Predator-Prey Interactions*, (pp. 240–255). Oxford University Press.
Spitzer, R., Felton, A., Landman, M., et al. (2020). Fifty years of European ungulate dietary studies: A synthesis. *Oikos, 129*, 1668–1680. https://doi.org/10.1111/oik.07435
Stiegler, J., von Hoermann, C., Müller, J., et al. (2020). Carcass provisioning for scavenger conservation in a temperate forest ecosystem. *Ecosphere, 11*, e03063. https://doi.org/10.1002/ecs2.3063
Theuerkauf, J., Jędrzejewski, W., Schmidt, K., et al. (2003). Daily patterns and duration of wolf activity in the Białowieża Forest, Poland. *Journal of Mammalogy, 84*, 243–253. https://doi.org/10.1644/1545-1542(2003)084%3c0243:DPADOW%3e2.0.CO;2
Theuerkauf, J., & Rouys, S. (2008). Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. *Forest Ecology and Management, 256*, 1325–1332. https://doi.org/10.1016/j.foreco.2008.06.030
Tobajas, J., Descalzo, E., Ferreras, P., et al. (2021). Effects on carrion consumption in a mammalian scavenger community when dominant species are excluded. *Mammalian Biology, 101*, 851–859. https://doi.org/10.1007/s42991-021-00163-w
Tucker, M. A., Böhning-gaese, K., Fagan, W. F., et al. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *science, 469*, 466–469. https://doi.org/10.1126/science.aam9712
Valente, A. M., Acevedo, P., Figueiredo, A. M., et al. (2020). Overabundant wild ungulate populations in Europe: Management with consideration of socio-ecological consequences. *Mammal Review, 50*, 353–366. https://doi.org/10.1111/mam.12202
Visscher, D. R., Walker, P. D., Flowers, M., et al. (2023). Human impact on deer use is greater than predators and competitors in a multiuse

recreation area. *Animal Behaviour, 197*, 61–69. https://doi.org/10.1016/j.anbehav.2023.01.003

Vojtkó, A. (1990) A Központi-Bükk déli előterének vegetációja. Fol Hist-nat Mus Matr, pp. 27–36

Young, A., Márquez-Grant, N., Stillman, R., et al. (2015). An Investigation of Red fox (*Vulpes vulpes*) and Eurasian Badger (*Meles meles*) Scavenging, Scattering, and Removal of Deer Remains: Forensic Implications and Applications. *Journal of Forensic Sciences, 60*, S39–S55. https://doi.org/10.1111/1556-4029.12554

Zimmermann, B., Nelson, L., Wabakken, P., et al. (2014). Behavioral responses of wolves to roads: Scale-dependent ambivalence. *Behavioral Ecology, 25*, 1353–1364. https://doi.org/10.1093/beheco/aru134