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RESEARCH PAPER

Temporal overlap of human and apex predator activity on wildlife trails and forest roads

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Abstract. The daily activity patterns of animals are modulated by external factors such as habitat selection, temporal niche selection, prey availability and predation risk. Furthermore, different species show a variety of responses to human disturbance; therefore, to understand the effects of human activities on wildlife, it is crucial to consider the disturbance characteristics (e.g. type, frequency, timing and location of human activity). Our objective was to evaluate whether vehicles on forest roads altered the daily temporal activity patterns of three apex predators; Eurasian lynx (*Lynx lynx*), the grey wolf (*Canis lupus*) and brown bear (*Ursus arctos*), using an extensive camera trap data set collected across a gradient of forest roads and wildlife trails in the Croatian part of the Dinaric mountains. We expected a low temporal overlap between humans and apex predators but predicted this even lower at sites where vehicles are present. Consistent with our expectations, the general overlap in temporal activity of all three apex predators and humans was low, the former being primarily active at night/dawn/dusk hours and the latter during daylight hours. In contrast, our results showed similarity in the temporal activity of all three predators on wildlife trails and forest roads where human activity was more frequent and diverse.

Key words: activity patterns, camera traps, *Lynx lynx*, *Canis lupus*, *Ursus arctos*

Introduction

The daily activity patterns of animals are considered to be affected by environmental and evolutionary factors (Halle 2000). That is, animals must adapt their physiology and behaviour to species-specific circadian rhythms that govern their daily activity (Kronfeld-Schor & Dayan 2003, Dibner et al. 2010, Heurich et al. 2014). In addition, circadian patterns are modulated by external factors such as habitat selection (Díaz-Ruiz et al. 2016), temporal niche selection (Chavez & Gese 2006), prey availability (Lucherini et al. 2009) and predation risk (Gliwicz & Dabrowski 2008). Several studies have reported that wildlife also shift their daily activity patterns in response to human disturbance, where animals avoid times of day when humans are the most active (George & Crooks 2006, Barrueto et al. 2014, Mysłajek et al. 2020). For example, some studies found that the impact of people on wildlife activity at wildlife crossing structures is highly context-dependent (Barrueto et al. 2014). Therefore, by observing changes in activity patterns, we can improve our understanding of ecological processes and the conservation implications of human disturbance on animals' activity (Gaynor et al. 2018).

Humans can impact apex predators the same way as they impact smaller predators and prey species through density-mediated (direct) and trait/behaviourally-mediated (indirect) pathways (Ordiz

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et al. 2013). A growing number of studies address the importance of anthropogenic effects on wildlife, including behavioural responses such as increased flight and vigilance (Mainini 1993, Naylor et al. 2009) or changes in spatial or temporal habitat use (George & Crooks 2006, Rogala et al. 2011), such as changing the activity patterns to avoid humans (Steven et al. 2011, Spaul & Heath 2016). Moreover, recent studies have suggested that fine-scale reactive avoidance strategies may promote coexistence among different species by minimising the risks of encounters (Swanson 2014). Thus, subordinate predator species may reactively alter their habitat use on a moment-to-moment basis (Swanson 2014) instead of pre-emptively avoiding large portions of the landscape or preferred habitat types, thus losing access to the resources therein (Broekhuis et al. 2013, Swanson 2014).

Temporal camera-trap data offers the opportunity to address unresolved questions regarding species ecology and community interactions, such as variation in activity patterns and partitioning along the temporal niche axis. These temporal insights also provide a better understanding of human-driven changes to species behaviours and interactions and the resulting impacts on temporal niche partitioning and community structure (Lewis et al. 2021). However, to understand the effects of human activities on wildlife, it is essential to consider the disturbance characteristics (e.g. type, frequency, timing, and location of human activity) and wildlife characteristics (e.g. species life history, age, and sex) (Lewis et al. 2021).

We studied the potential impacts of human activity (i.e. cars, hikers, bikers) on three apex predators – Eurasian lynx (*Lynx lynx*), the grey wolf (*Canis lupus*) and brown bear (*Ursus arctos*) in Croatia, Europe. The distribution area of the three large carnivores in Croatia mostly overlaps and coincides with the Dinaric mountain chain. The brown bear population in Croatia is estimated at 1,000 individuals (Huber et al. 2019), and the lynx population is estimated at a minimum of around 90 adult animals (Gomerčić et al. 2021), while there is no scientifically based estimation of the number of wolf packs. In this study, our main objective was to evaluate whether motorised human activity on forest roads altered animals' daily temporal activity patterns. We predicted that animal temporal activity would be negatively related to human activity, and we assumed that observed carnivores might exhibit different activity patterns on forest roads compared to forest trails where there is no motorised human activity.

Material and Methods

Study area

Our study was conducted in the Gorski kotar, Lika and northern Dalmatia region (Croatia, Europe), with a total surface area of the study region of around 6,354 km^2. This area is a part of the Dinaric mountain range, where the distribution of all three apex predators overlaps. In this region, the altitudinal range is pronounced, ranging from sea level up to the highest point, 1,757 m, at the summit of Mount Velebit. Predominant habitats are rugged karst terrains with mixed forests of European beech (*Fagus sylvatica*) and mixed oak forests that dominate at medium and low. The dominant canopy tree species of the mountain conifer forests are spruce (*Picea abies*), silver fir (*Abies alba*), and black pine (*Pinus nigra*) (Župan Hajna 2019).

The area has two climate types: moderately warm and humid with warm summers and wet boreal in the altitudinal zone above 1,200 m. Average annual rainfall of 1,500-2,000 mm and an annual temperature averaging 5-8 °C, ranging from a maximum of 32 °C in July to a minimum of −20 °C in January, characterise this ecoregion (Šegota & Filipčić 2003).

Besides the three apex predators, the golden jackal (*Canis aureus*) is also present in the area (Krofel et al. 2022), as well as several species of medium and smaller carnivores (Topličanec et al. 2019).

Data collection

A network of camera traps was set along Gorski kotar, Lika and the northern Dalmatia region in Croatia. The study area was gridded into 10 × 10 km cells, and at least one camera trap was installed in each cell along wildlife trails and forest roads that wild animals tended to use.

Our sampling was passive as we did not use attractants (i.e. sight, sound, scent) to lure animals to the camera location. Forest roads were built chiefly for forestry purposes and are usually covered in gravel, while wildlife trails are pathways worn by the movement of humans and animals. Forest roads are wider and usually flat, while trails are narrow and covered by rocks and roots. We also distinguish them based on the possibility of vehicle movement – only non-motorised human activity was possible on wildlife trails, whereas on forest roads, both motorised and non-motorised human activity could be observed.

Cuddeback model 1224 and Acorn LTL 6511 were used with the following technical settings: activation

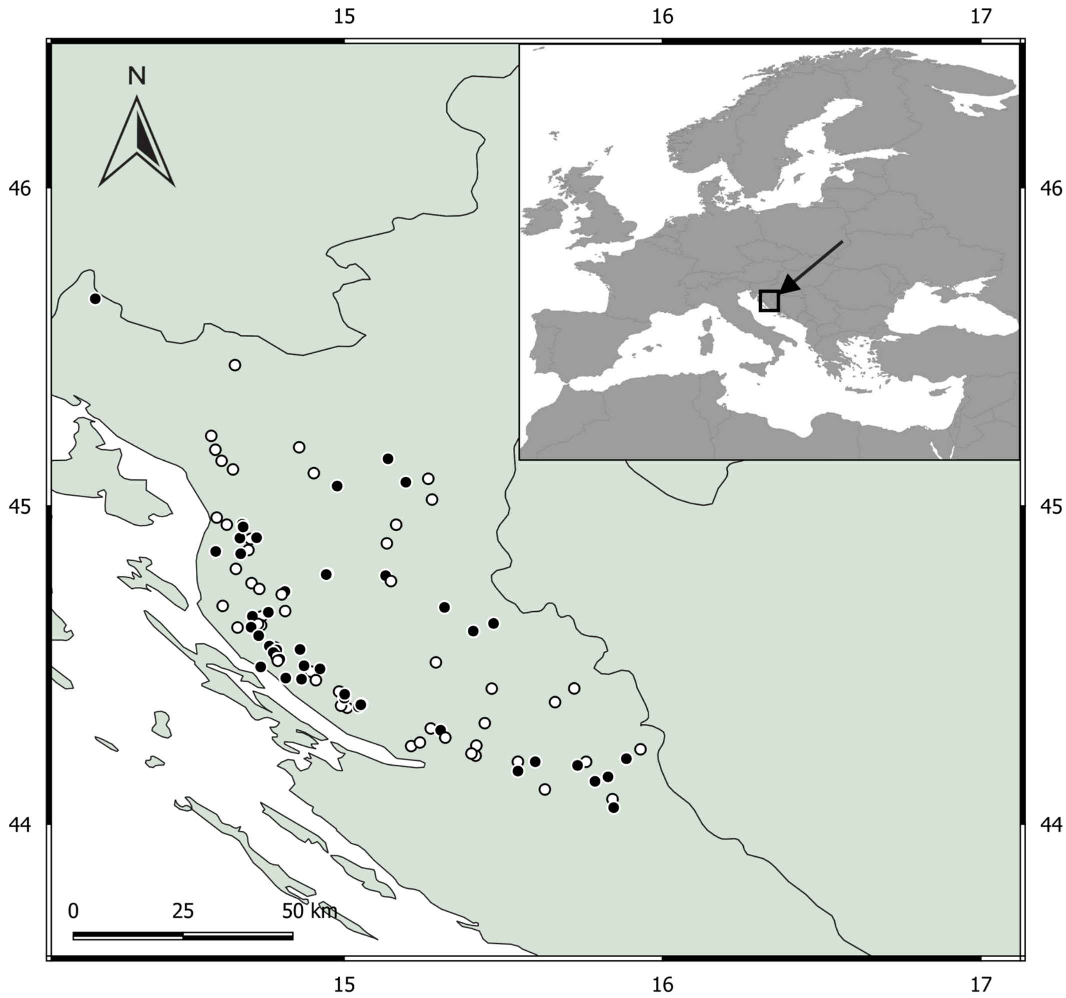

Fig. 1. Locations of camera traps set on wildlife trails and forest roads in Croatia active in the period February 12th 2018 – September 8th 2021 (43 months); the colour of dots represent different location types: black dots – forest road (n = 66); white dots – wildlife trail (n = 31). On average, each camera trap was active for 235 days.

speed 0.25 s, camera resolution 5 and 12 MP, flash with infrared light (wavelength IR, 850 nm), wide range. Camera traps were set to record one photo and 30 seconds of video or three photos without the video. During the period from the 12th of February 2018 to the 8th of September 2021 (43 months), camera traps were set at 97 locations, of which 66 were set on forest roads and 31 on wildlife trails (Fig. 1). Our intention was for camera traps to remain at each location all year round. However, due to malfunctions, theft, snow or intensive logging, some were not active during the entire research period at the selected locations or were moved to another location in the same grid cell. The minimum distance between two camera trap locations was at least 1 km, and only one camera trap was active at each 10 × 10 km cell at the same time. For that reason, only active days were considered in the analyses. Camera traps were active for 22,790 days, an average of 235 days per camera trap during the study period. The cameras were programmed to record the time and date for each photograph. Camera traps were visited at least every two months to replace memory cards and batteries. Photographs were processed using the camera trap software Camelot (Hendry & Mann 2018), while empty photographs were selected and erased before uploading into Camelot. On each photograph, we identified the species, the number of animals, age category (juvenile or adult) and sex (if possible). Additionally, we checked the videos to estimate the number of wolves in the pack, the number of lynx kittens and the number of brown bear cubs. As the sample size was too small when the data was grouped according to the animals' age and sex, we have not included those factors in our analysis. To avoid inflated counts caused by repeated detections of the same animal, we defined the same species captured within 10 minutes as one event (Rovero & Zimmermann 2016).

Data analysis

According to Rowcliffe et al. (2014), we defined activity records as the time within the 24 h period when camera

Table 1. Summary of camera trap records and the number of observations of humans and apex predators on wildlife trails and forest roads. Wildlife trails include non-motorised human activity, whereas forest roads include motorised and non-motorised human activity.

	Total number of observations	Wildlife trails	Forest roads	No. of cameras with observed species on wildlife trail (n/%)	No. of cameras with observed species on forest road (n/%)
Human	6,014	634	5,380	43 (81.1 %)	43 (97.7 %)
Lynx	222	57	165	20 (37.7%)	23 (52.3 ,5%)
Grey wolf	147	48	99	18 (34.0%)	20 (45.5%)
Brown bear	679	283	396	42 (79.2 %)	38 (86.4 %)

traps recorded a given species. We split data into two categories: forest roads and wildlife trails, based on the location of the camera trap. Human activity records on forest roads comprise pooled observations of motorised and non-motorised activity.

We evaluated the temporal overlap in activity patterns of three apex predator species with the daily human activity patterns on forest roads and wildlife trails using the software R (R Core Team 2021). We used the package Overlap, which estimates the coefficient of overlapping (Δ) by applying kernel density functions to two temporal data sets and presents them visually by plotting them (Meredith & Ridout 2021). The coefficient of overlap (Δ) can be interpreted as the integrated difference in estimated density functions for two distributions and thus ranges from 0 (no overlap) to 1 (complete overlap) (Ridout & Linkie 2009). Estimator Dhat4 (Δ_4) is recommended if both samples are greater than 50; otherwise, the Dhat1 estimator needs to be used. Our sample size for each species was > 50; therefore, we used the Δ_4 estimator as recommended (Meredith & Ridout 2021). Within the Overlap package in R, we generated 10,000 smoothed bootstrap samples to estimate a mean coefficient of overlap and 95% confidence intervals for each species pairing (Meredith & Ridout 2021).

To evaluate the statistical significance of overlap in temporal activity patterns of humans and three apex predators, we used the Wald test in the Activity package (Rowcliffe 2022) in R. Also, to cross-validate the results, we used the TimeOverlap 1.0 software (Castro-Arellano et al. 2010), which calculates Pianka and Czehanowski indices of overlap among several distributions.

Results

During 22,790 camera trapping days across 97 camera sites in Croatia, we obtained 7,062 independent observations of apex predator species (*Lynx lynx*, *Canis lupus*, *Ursus arctos*) and humans on forest roads and wildlife trails. Human activity comprised 6,014 independent observations (85.2%), while we obtained 222 activity records for lynx (3.1%), 147 for wolves (2.1%) and 679 for brown bears (9.6%) across all sites (Table 1).

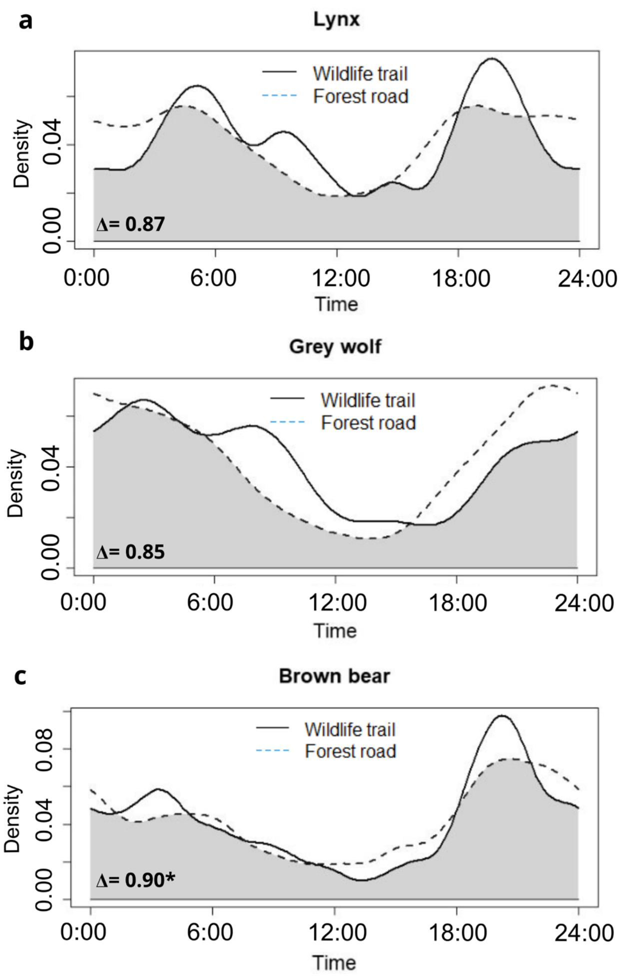

Fig. 2. Daily activity patterns of Eurasian lynx (a), grey wolf (b) and brown bear (c) on wildlife trails (solid line) and forest roads (dashed line). Time of day is presented on the x-axis, and activity, measured by kernel density, is presented on the y-axis. The shaded area corresponds to the coefficient of overlap (Δ). Wald test *P* values indicate statistical significance (**P* < 0.05, ***P* < 0.001).

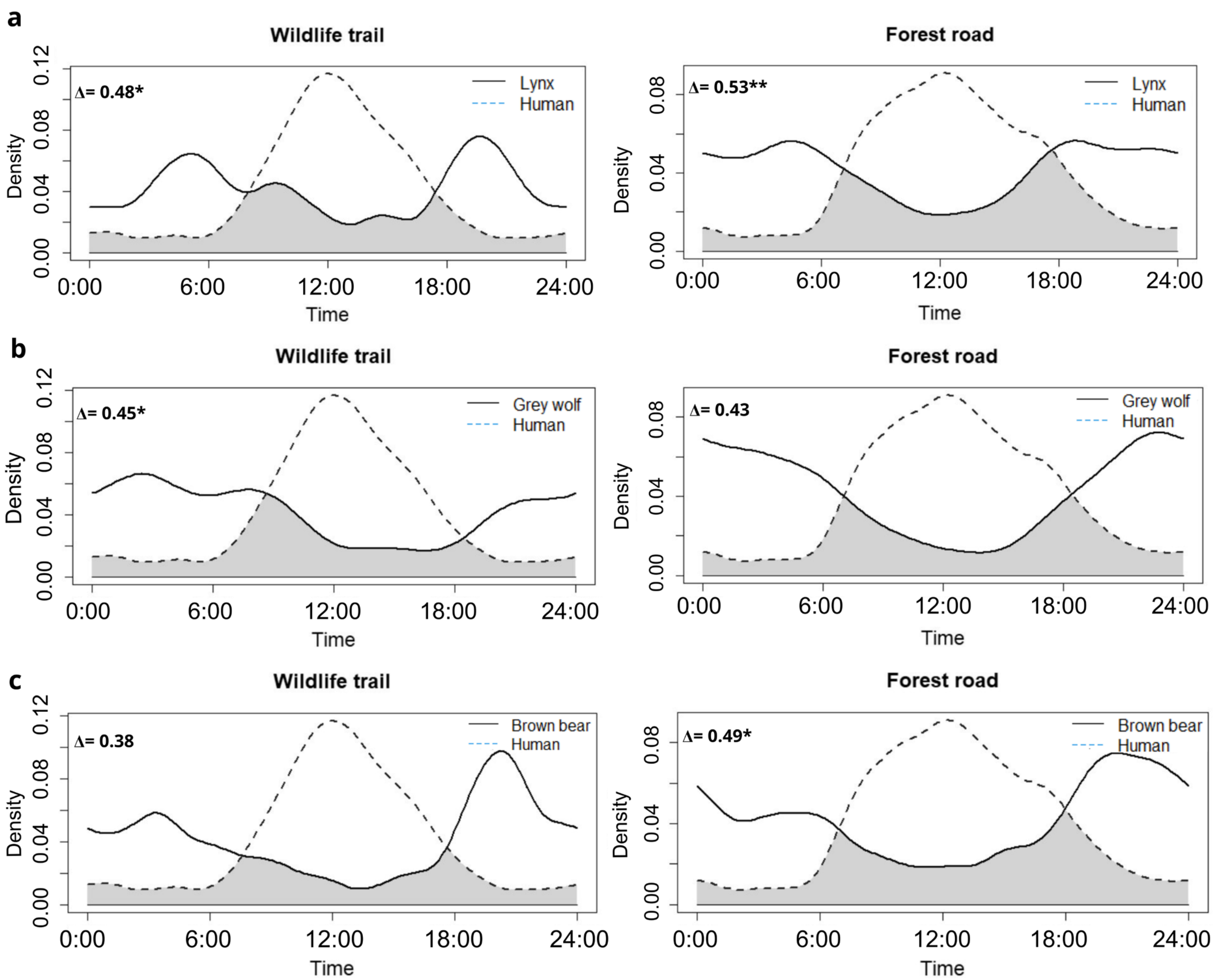

Fig. 3. Temporal overlap between Eurasian lynx (a), grey wolf (b) and brown bear (c) (solid line) compared with human activity (dashed line) on wildlife trails and forest roads. The time of day is presented on the x-axis, and activity, measured by kernel density, is presented on the y-axis. The shaded area corresponds to the coefficient of overlap (Δ). Wald test *P* values indicate statistical significance (**P* < 0.05, ***P* < 0.001).

Human activity on wildlife trails included non-motorised activity, while on the forest roads, human activity comprised motorised (cars, motorbikes, trucks, tractors, logging machinery; used for professional and recreative activities) and non-motorised activity and was 3.5 times more frequent compared to wildlife trails (Table 1). Motorised activity comprised 28.0% of the total human activity on forest roads.

Interspecific time use

Results showed general human activity primarily from 6 to 18 hours (91.7%) and relatively minimal activity from 18 to 6 hours (8.3%). Observed carnivores were merely active during nocturnal and crepuscular hours (from 18 to 6 hours; lynx: 65.3%, grey wolf: 72.8% and brown bear: 71.0%) (Fig. 2). Conversely, humans were more frequent (77.9%), and for a broader range of activities, on forest roads compared to wildlife trails (Fig. 3), with activity peaking just around noon on both types of micro-locations.

We tested our data using three different statistical methods – Wald test, Pianka and Czehanowski indices. The results of the Wald test *vs.* Pianka and Czehanowski were not complementary, and we interpreted the results based on the Wald test. For the three predator species, we analysed 1) overlap coefficient of temporal activity between each predator species and humans on wildlife trails, 2) overlap coefficient of temporal activity between each predator and humans on forest roads and 3) coefficient of overlap in activity pattern between wildlife trails and forest roads for each predator species.

Comparison of activity patterns of lynx and humans both on wildlife trails and forest roads showed a statistically significant difference in both locations, with more notable statistical significance in activity on forest roads (Table 2, wildlife trail: W = 4.27, $P = 0.04$, forest road: W = 16.2, $P < 0.001$). However, when we tested the coefficient of overlap between lynx activity

Table 2. Coefficient of overlap (Dhat), CI (95%), Wald test (W) for temporal overlap between humans and three observed apex predators.

		CI (95%)		
Species	Dhat	Upper	Lower	W
Wildlife trail				
Lynx	0.48	0.37	0.58	4.27*
Grey wolf	0.45	0.33	0.56	8.31*
Brown bear	0.38	0.33	0.43	1.97
Forest road				
Lynx	0.53	0.47	0.59	16.20**
Grey wolf	0.43	0.35	0.50	3.21
Brown bear	0.49	0.44	0.53	4.78*

*Significant *P* values (i.e. $P < 0.05$).
**Significant *P* values (i.e. $P < 0.001$).

Table 3. Comparison of temporal activity patterns of three apex predators on wildlife trails and forest roads: coefficient of overlap (Dhat), CI (95%), Wald test (W).

		CI (95%)		
Species	Dhat	Upper	Lower	W
Lynx	0.87	0.77	0.96	2.82
Grey wolf	0.85	0.74	0.97	0.19
Brown bear	0.90	0.85	0.95	4.23*

*Significant *P* values (i.e. $P < 0.05$).

patterns on wildlife trails and forest roads, we found no significant difference ($\Delta 4 = 0.84$, W = 2.82, $P = 0.09$). On wildlife trails, lynx showed a peak in their activity around 20 h, and after dropping around 23 h, it stayed constant throughout the night. The second peak of activity was observed in the early hours of the day, around 5 h (Fig. 2a). On forest roads, graphs showed more frequent lynx activity during the night, where activity was constant until 5 h (Fig. 2a).

A comparison of temporal activity between grey wolves and humans on wildlife trails showed a statistically significant difference (Table 2, W = 8.31, $P = 0.004$), while the difference in activity of wolves and humans on forest roads were not statistically significant (W = 3.21, $P = 0.07$). Furthermore, when we compared wolf activity patterns between wildlife trails and forest roads, there was no significant difference (Table 3, W = 0.19, $P = 0.66$). Wolves were more active during the early hours of the day, with the lowest activity just after noon, then rising in the later part of the day (around 18 h) and peaking between midnight and 6 h on forest roads, while activity on wildlife trails started dropping later, around 8 h (Fig. 2b).

Brown bear activity was the lowest around noon. A strong peak of activity was evident around 20 h, then dropped around 23 h and stayed high during the night (Fig. 2c). There was no significant difference in activity of brown bears and humans on wildlife trails (Table 2, W = 1.95, $P = 0.16$), while the difference in activity on forest roads was statistically significant (W= 4.78, $P = 0.02$). We observed a high coefficient of overlap (Dhat4 = 0.90) when comparing activity patterns of brown bears in the locations, which was statistically significant (Table 3, W = 4.23, $P = 0.04$).

Discussion

Understanding how humans and large carnivores might coexist is an increasingly common goal (Cohen 2003, Theobald 2005, Seto et al. 2012). Professional and recreational activities (logging, hunting, hiking, off-road biking, picking mushrooms and plants) on forest roads are bringing humans to the most remote areas of large carnivore habitats, and the capacity of carnivores to avoid humans is vital to limit adverse outcomes to human-carnivore encounters (Oriol-Cotterill et al. 2015, Lamb et al. 2020). Although forest roads usually have too little traffic to pose a significant risk of wildlife-vehicle collisions (Ripari et al. 2022), disturbance caused by vehicles in the core of their habitat may still alter carnivore activity (Suárez-Esteban et al. 2013, Turk et al. 2021). Consequently, we examined the potential difference in the influence of motorised and non-motorised human activity on the three largest European carnivores in their natural habitat in the Croatian part of the Dinarics. To evaluate the statistical significance of overlap in temporal activity patterns of humans and three apex predators, we used the Wald test and Pianka and Czehanowski indices calculated in TimeOverlap 1.0 software (Castro-Arellano et al. 2010). Unfortunately, the Pianka and Czehanowski indices were not sufficiently sensitive for our dataset, as they depended on the number of columns set in the histogram. So, we interpreted our results based on the Wald test, which showed a general overlap in temporal activity of all three apex predators and humans was low, but to a different extent, with predators being predominantly active at night/dawn/dusk hours while humans were primarily active during daylight hours. Activity patterns of lynx and humans differed significantly in both locations. A statistically significant difference in activity patterns among wolves and humans was observed only on wildlife trails, while activity patterns of wolves have not changed between the habitats, indicating that human activity is causing the difference in wolf activity patterns between wildlife trails and forest roads. Conversely, bears showed a statistically significant difference in response to human temporal activity on forest roads.

Our analysis showed that out of the three researched species, only brown bears display a statistically significant difference in temporal activity on wildlife trails and forest roads. However, this difference was most prominent at dusk and dawn, when human activity was low. Thus, we can conclude that motorised-human activity did not influence the temporal activity of the three large carnivores in our study area. These results are consistent with Mori et al. (2020), who found that it was unlikely that humans altered the activity patterns of wolves, even in areas with high human occurrence.

It should be considered that mechanisms of coexistence may be dynamic, and future studies are required to clarify whether other factors (such as age, sex or season of the year) play a role in shaping the activity patterns of the observed species in response to human activity. For example, some animals might exhibit bolder or more naive behaviour (e.g. young animals and males), whereas other animals might be warier of human disturbance (e.g. adult females with offspring, Knight & Gutzwiller 1995). Although our study did not allow us to evaluate these relationships, our results are helpful in evaluating and predicting the degree to which predators might be influenced by human activity in their core habitat.

Mitigating and managing the potential adverse effects of human-wildlife interactions will be a continual challenge (König et al. 2020). Including spatiotemporal behaviour in management plans may help promote coexistence and reduce the conflict between humans and wildlife (Mori et al. 2020). While we cannot wholly define the extent of the influence of humans on the temporal activity pattern of predators on forest roads, or identify fine-scale avoidance, given that the data in our study were grouped and, therefore, could not demonstrate fine-scale behavioural responses, such an analysis might facilitate the design and implementation of wildlife management plans in landscapes with high levels of human activity. Our study area, the Croatian part of the Dinaric mountain chain, is intersected by a dense network of non-paved forest roads (Pentek et al. 2007), primarily built for logging but increasingly used for other purposes. Studies like this can help understand the tipping points at which human activity becomes detrimental to biodiversity, ecosystem function and conservation efforts (Haswell et al. 2020).

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Author Contributions

T. Gomerčić and M. Sindičić conceived and designed the study. S. Blasković, T. Gomerčić and I. Topličanec participated in fieldwork with the support of other colleagues mentioned in the Acknowledgements. S. Blašković and T. Gomerčić analysed the data while all authors wrote the manuscript.

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