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Research article

The diel niche of brown bears: constraints on adaptive capacity in human-modified landscapes

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Diel activity rhythms, representing the behavioral pattern of the sleep–wake cycle, may be adjusted by wildlife in response to changes in environmental conditions. An increase in nocturnality is typically recognized as an adaptive strategy to segregate from humans and mitigate heat stress. Numerous studies have investigated spatial patterns and habitat use of large carnivores in human-modified landscapes, but little research has examined their activity rhythms. We compiled Global Positioning System data (2004–2022) for 139 brown bears *Ursus arctos* from six populations across Europe, representing a human-modified landscape, and the Greater Yellowstone Ecosystem, U.S.A., representing a landscape with limited human impact, which we used to calculate hourly movement rates as an activity proxy. Using a Bayesian approach to model the temporal autocorrelation of activity data, we tested if the extent of nocturnality in brown bears is modulated by intensity of human encroachment, accounting for primary productivity and maximum ambient temperature. All bear populations exhibited a predominantly bimodal, crepuscular pattern of activity, although Yellowstone bears were proportionally more crepuscular and diurnal. Whereas the effect of primary productivity was variable, all European populations became more nocturnal in response to higher human encroachment and reduced diurnal and crepuscular activity at higher summer temperatures, decreasing overall diel activity levels. Yellowstone bears displayed the greatest shift towards nocturnality among all populations in response to increasing human encroachment, and increased nocturnal activity to compensate for

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lower diurnal and crepuscular activity at higher summer temperatures. Our research indicates that European bears in human-modified landscapes may be reaching a limit in the behavioral plasticity they can manifest in their activity patterns, being already constrained into increased nocturnality. Our findings enhance the understanding of brown bear adaptive capacity to accommodate future changes, such as urbanization and increasing temperatures, to the ecosystems they inhabit.

Keywords: anthropocene, behavioral plasticity, diel activity rhythms, human encroachment, GPS telemetry, *Ursus arctos*

Introduction

Human activity impacts wildlife at different scales and can influence multiple aspects of their ecology such as movements, distribution, resource use, and daily patterns of activity (Dirzo et al. 2014, Gaynor et al. 2018, Mumme et al. 2023). In mammals, circadian timing of activity stems from a complex system of endogenous mechanisms, including gene expression, that act as biological clocks (Partch et al. 2014, Sanchez et al. 2022). Yet, reception of external stimuli and their integration within endogenous time-keeping processes is a fundamental aspect ensuring survival and reproduction in the wild (Helm et al. 2017). Indeed, the distribution of animal activity throughout the diel period (i.e. their diel niche; Hut et al. 2012) represents a crucial element in their adaptation to variation and changes in environmental conditions (Helm et al. 2017, Rattenborg et al. 2017). Being active during certain hours of the diel period can aid animals in thermoregulation and the optimization of foraging efficiency, and can favor intra-specific interactions (e.g. mating) while avoiding competitors or predators (Terrien et al. 2011, Helm et al. 2017, Kronfeld-Schor et al. 2017).

Temporally segregating from humans through increased nocturnality is acknowledged as an adaptive strategy in wildlife for enhancing survival in highly modified landscapes (Gaynor et al. 2018, Cox et al. 2023), where opportunities for spatial segregation are limited. Encounters with humans may generate a flee response, potentially impacting foraging opportunities and energy balance (Karasov 1992, Lasky and Bombaci 2023). Thus, a human-induced shift towards nocturnality may promote coexistence in human-dominated landscapes by decreasing the likelihood of direct interactions with humans, including animal–vehicle collisions and instances of conflict (Gaynor et al. 2018, Kautz et al. 2021, Cox et al. 2023). However, human-caused disruption of diel activity rhythms of animals may contrast with the inherent rhythmicity of behavioral and physiological processes, such as the regulation of body temperature and metabolic rate (Refinetti 2020), and hormonal release (Gamble et al. 2014). This mismatch may impact the fitness of individuals, undermine their capacity to adapt to changing environmental conditions, and ultimately impact long-term viability of populations (Libert et al. 2012, Walker et al. 2019). Future trends in urban growth and land development may threaten the 2050 goals to slow biodiversity decline set by the Global Biodiversity Framework (IPBES 2019, CBD 2021), with predictions indicating that most ecoregions will face considerable loss of natural habitats (i.e. biological communities formed by native plant and animal species and where human activity has not essentially modified the area's primary ecological functions; www.eea.europa.eu/help/glossary/eea-glossary; Ren et al. 2023). This outlook emphasizes how evaluating wildlife behavioral plasticity and adaptations to increasing human encroachment in natural landscapes can inform conservation efforts (IPBES 2019).

From an evolutionary perspective, large carnivores have generally experienced little or no predation risk from other species, but they currently face considerable risk of mortality by humans and many large carnivores are threatened across their range (Ripple et al. 2014). Their slow reproductive rates and extensive home ranges make large carnivores highly susceptible to anthropogenic landscape modifications, such as land conversion and fragmentation (Ripple et al. 2014). Therefore, large apex predators may display more risk-averse responses to human encroachment compared with other wildlife (Burton et al. 2024). Indeed, large carnivores are reported to be more sensitive to human presence than other trophic groups, as they may exhibit substantial shifts in their diel niche to reduce overlap with human activity (Frey et al. 2020, Burton et al. 2024). Research on the ecology of large carnivores and their adaptive response to human encroachment has generally prioritized the spatial dimension and resource use (Tucker et al. 2018, Hertel et al. 2025). Recent efforts, however, have begun to focus on understanding how the diel niche of large carnivores might shift in response to human disturbance and potential implications for fitness (Frey et al. 2020, Cox et al. 2023, Vicedo et al. 2023).

Brown bears *Ursus arctos* are one of the world's most widely distributed and conflict-prone large carnivores, due to their large size and omnivorous diet (Bojarska and Selva 2012, Swenson et al. 2023). Recent studies have indicated that brown bears living in the human-modified landscapes of Europe tend to be more crepuscular and nocturnal compared with bears in North America, where they generally experience relatively lower human disturbances (Zedrosser et al. 2011, Morales-González et al. 2020). Nevertheless, to date, no study has directly contrasted diel activity patterns of brown bear populations experiencing a gradient of anthropogenic impact across the two continents to infer the extent of their behavioral plasticity in adapting diel activity to local conditions.

Higher levels of human footprint, measured as density of infrastructures or human settlements, or tourist pressure in nature reserves among other proxies, have been associated in both Europe and North America with an increase in brown bear nocturnal activity (Ordiz et al. 2013, Anderson et al.

2023). Diel activity may be further modulated by seasonal life history events, such as mating (Steyaert et al. 2013) and hyperphagia (i.e. a period of intense eating to increase body mass before bears hibernate in winter; González-Bernardo et al. 2020), among other factors, such as age class (Kaczensky et al. 2006, Hertel et al. 2017), ambient temperature (Seryodkin et al. 2013, Rogers et al. 2021), and seasonal shifts in diet (Fortin et al. 2013, McLellan and McLellan 2015). For instance, younger individuals may access resource-rich areas by exploiting times of day when dominant bears are less active to avoid conflict (Hertel et al. 2017, Kilfoil et al. 2023). Indeed, seasonal food availability and food type play key roles in shaping diel behavior of brown bears (Ware et al. 2012, Hertel et al. 2025). Fortin et al. (2013) reported that, when feeding primarily on elk calves during spring and early summer, brown bears in the Greater Yellowstone Ecosystem (hereafter, Yellowstone; Craighead 1991) were nocturnal, whereas they became more crepuscular and diurnal during late summer and fall, when feeding on roots and pine nuts. This indicates that bears likely adjust their daily patterns of activity depending on variations in their efficiency at acquiring seasonal key foods throughout the diel period. Additionally, the spatial distribution of key bear foods may influence where activity of bears takes place (Munro et al. 2006). For instance, during hyperphagia, foraging activity on hard mast has often been associated with areas of high primary productivity, typically indexed by the normalized difference vegetation index (NDVI; e.g. in Yellowstone and Cantabrian, i.e. northern Spain, brown bears; Costello et al. 2014, Pérez-Girón et al. 2022). Ambient temperature has also been reported to influence brown bear activity rhythms, although results differ geographically. For example, in British Columbia, Canada, no relationship was found between daily maximum temperatures and diurnal or nocturnal activity (McLellan and McLellan 2015), whereas bears on the Sikhote-Alin mountains in Russia increased nocturnality during the hottest summer days (Seryodkin et al. 2013).

In this study, using hourly movement rates as a measure of activity, we assessed the effect of human encroachment on diel activity patterns of brown bear populations at a transcontinental scale, controlling for seasonal primary productivity, and daily maximum ambient temperature. We selected bear populations to represent differences in the extent of human encroachment, which we measured using a composite index representing landscape modification and human population density. Yellowstone brown bears, which reside in a large and relatively undisturbed temperate ecosystem, were used as a reference population to contrast with bears living in the human-modified landscapes of Europe (Zedrosser et al. 2011).

We predicted that: (P1) brown bears in European populations, during their annual active period, display greater nocturnality compared with Yellowstone bears, in their attempt to temporally segregate from humans; (P2) greater human encroachment prompts proportionally greater shifts towards nocturnal and crepuscular activity and a corresponding decrease in diurnal activity in bears; (P3) during hyperphagia, bears increase activity during diel activity periods in resource-rich areas, as indexed by primary productivity depending on predominant feeding patterns; lastly, (P4) during summer months, when heat stress is most likely, higher maximum temperatures prompt an increase in bear nocturnal and crepuscular activity at the expense of diurnal activity to avoid hyperthermia.

Material and methods

Compilation and screening of GPS datasets

We compiled Global Positioning System (GPS) data from six brown bear populations (i.e. Apennine, Karelian, Scandinavian, Yellowstone, and Dinaric Pindos bears from Croatia and Serbia), spanning 11 countries, collected during 2002–2022 (Fig. 1). Scandinavian and Karelian bears were included to represent bears residing in landscapes featuring relatively low human development, but experiencing intense hunting practices (Fig. 2; Supporting information). The other European bear populations were chosen along a latitudinal gradient, different management systems, and

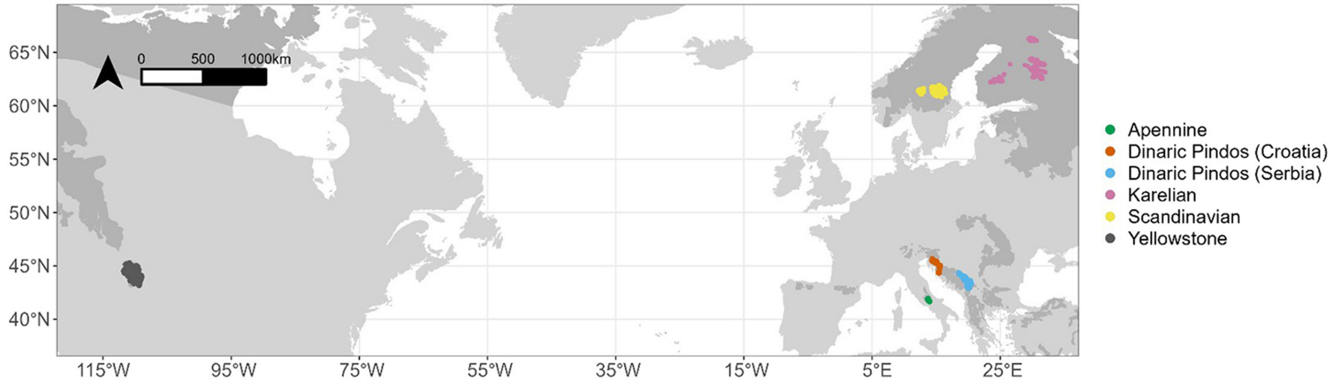

Figure 1. Distribution of GPS locations of 332 brown bears from six populations in Europe and North America (2002–2022, Massicotte et al. 2023). Dark gray regions display the species range (McLellan et al. 2017).

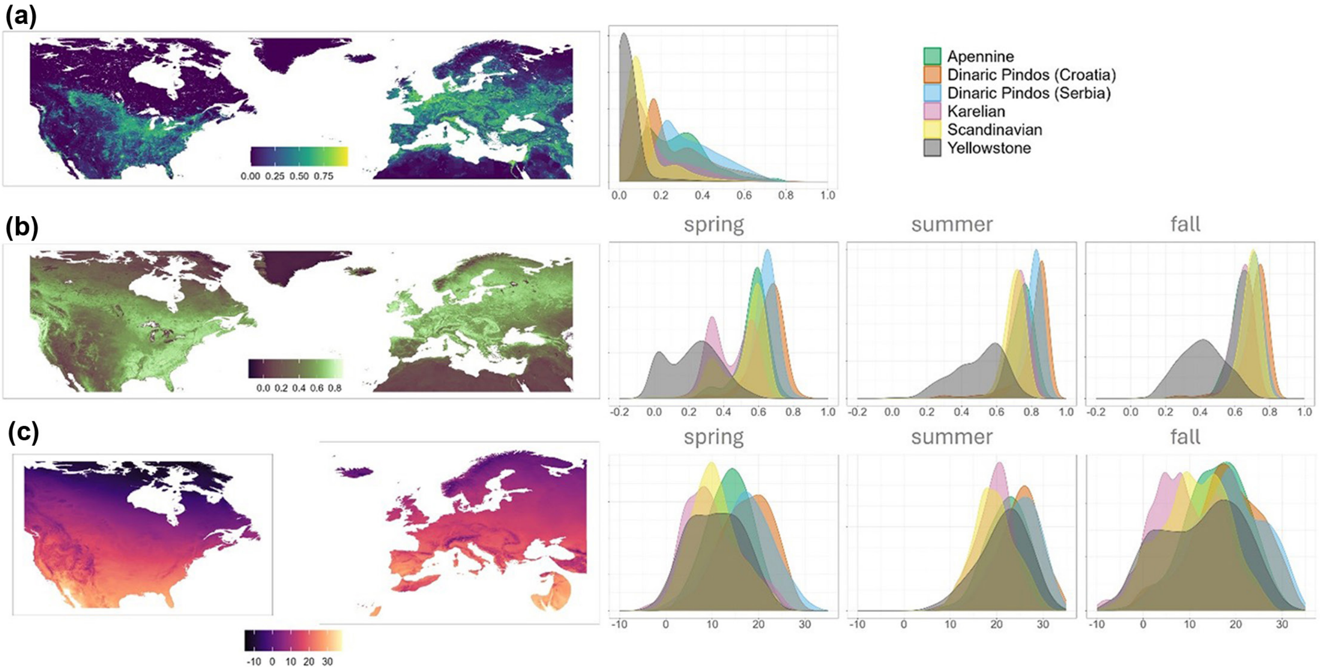

Figure 2. Distribution maps (left panels) and density plots of within population availability (right panels) for each covariate used to model diel activity patterns of bear populations across Europe and North America: (a) global human modification of terrestrial systems (GHM; Kennedy et al. 2020), (b) seasonal normalized difference vegetation index (NDVI; Didan 2021), and (c) daily maximum ambient temperature (Thornton et al. 2022, Cruz-Alonso et al. 2023). Whereas the GHM layer does not vary temporally, the distribution maps of NDVI and daily maximum temperature refer to values averaged across 2015. Available values shown in density plots are extracted from each pixel available in the minimum convex polygon of bear locations in each population during the sampling period of the original dataset (overall, 2002–2022).

ecological conditions, including bears from Croatia, Serbia, and central Italy (Fig. 2; Supporting information). European bear populations were contrasted with bears in Yellowstone, that represent a protected population living in a largely unaltered environment. Overall, the dataset comprised 6 348 667 GPS locations from 164 female and 168 male bears (Supporting information). None of the individuals were collared in response to human–bear conflicts, as activity patterns of these bears may reflect human-related bear behaviors (e.g. habituation, food-conditioning).

To allow comparisons across bear populations, we limited our analyses to the annual period of activity, which we defined as 1 April to 30 November (González-Bernardo et al. 2020). Additionally, since some bears began denning earlier or remained in their den longer, we calculated the distances between consecutive mean daily positions to exclude stationary locations in the weeks before 30 November or after 1 April (Supporting information). To verify our predictions, we divided the year into three seasons, approximately encompassing changes in diet, mating behavior, climatic conditions, and management practices (Supporting information): spring, including the post-denning period, from 1 April to 31 May; summer, including the mating period, from 1 June to 31 July; fall, including hyperphagia and bear hunting periods, from 1 August to 30 November.

To remove potential outliers from trajectories of individual bears, we screened the dataset using the process described in Bjørneraas et al. (2010), and accordingly removed < 1% of GPS locations per bear population (Supporting information). Additionally, assuming dispersing bears could display different activity patterns compared with resident ones, we used net squared displacement curves computed by the ‘migrateR’ package (www.r-project.org, Spitz et al. 2017) to identify dispersers that were subsequently excluded from the final dataset (Supporting information). Due to constraints in computational resources and time, we had to subsample the number of bears from each population, but still retained an adequate number of individuals for meaningful population-level inference. We selected approximately 20 bears from each European population, prioritizing those with larger datasets, while ensuring a balanced sex ratio in each sample (Supporting information). For the Yellowstone population, instead, we retained 43 individuals, to allow a more precise estimate of their activity patterns, serving as the reference for comparing diel activity of European bears. Finally, to ensure a comparable GPS acquisition rate across bears and populations, we subsampled the dataset at an acquisition rate of 1 location hour^{-1} (Supporting information). The final dataset therefore comprised 379 676 GPS locations collected from 139 bears, for an equivalent of 235 bear-years, from 2004 to 2022 (Supporting information). We subsequently calculated hourly movement rates (km h^{-1}) to use as a metric of activity (Hertel et al. 2017, Bogdanović et al. 2021; Supporting information).

Environmental covariates

To assess the potential effect of human encroachment on diel activity patterns, we used global human modification of terrestrial systems (GHM) data (1 km resolution; Fig. 2; Kennedy et al. 2020). This index summarizes 13 anthropogenic stressors (i.e. population density, built-up areas, cropland, livestock, major roads, minor roads, two-track roads, railroads, mining/industrial areas, oil wells, wind turbines, powerlines, nighttime lights) in a value from zero (pristine) to one (highly modified). As a measure of primary productivity, we used the MODIS NDVI (1 km resolution; Fig. 2; Didan 2021). We aggregated and averaged NDVI on a seasonal basis for each year in the study period (i.e. 2004–2022). Lastly, to evaluate the effect of temperature on bear activity rhythms during summer, we employed daily maximum ambient temperature (McLellan and McLellan 2015). This was obtained from the Daymet dataset (1 km resolution; Thornton et al. 2022) for Yellowstone, and from data in the 'easyclimate' R package (www.r-project.org, 1 km resolution; Cruz-Alonso et al. 2023) for Europe, in the years 2004–2022 (Fig. 2) (see the Supporting information for further information).

We extracted GHM, NDVI, and temperature values at each bear location using the 'terra' package (Hijmans 2024) in R (www.r-project.org). For modeling purposes, we assumed that the value associated with each hourly bear location was representative of the environment experienced by the bear during the following hour.

Model development

To test our predictions, we used a Bayesian modeling approach, which does not require strict assumptions about parameter normality and allows flexibility in the formulation of the models without loss of precision (Clark 2005). We used Stan programming language (Stan Development Team 2024a) through the 'rstan' R package (www.r-project.org, Stan Development Team 2024b) for model development.

The general structure of the models was as follows (Donatelli et al. 2022):

$$y_{tpk[p]} = \alpha + \lambda^{*}_{tp} + \theta_{ph} \cdot z_{tk[p]} + \omega_{k[p]} + \varepsilon_{tpk[p]}, \tag{1}$$

where $y_{tpk[p]}$ is the hourly movement rate (km h^{-1}), with t identifying the date and time of each GPS location, p the bear population (Fig. 1), and k[p] the individual bear identifier nested within population. Therefore, each combination of bear and population corresponds to a unique value of k[p], accounting for residual variance associated with differences among individuals. The intercept is represented by α, whereas λ^{*}_{tp} represents a formula which varies depending on the model (Table 1) and contains the cyclical effect of hour of the day (below). To account for variation in daylight hours among study areas, we included a linear effect of daylength in all models (Ordiz et al. 2014). We extracted values of daylength for each bear location and associated day using R package 'chillR' (www.r-project.org, Luedeling et al. 2023). The effect of daylength on hourly movement rates is represented by $\theta_{ph}.z_{tk[p]}$, where $z_{tk[p]}$ is the value of daylength and θ_{ph} is the associated coefficient, that was modeled as an interaction with the bear population and hour of the day (i.e. $h = 1, \ldots, 24$). The parameter $\omega_{k[p]}$ is the random effect of individual ID nested within population, which is distributed according to a normal function with expected value 0. We used a different variance for each bear population ρ^2_p to account for possible differences in inter-individual variability across populations. Lastly, $\varepsilon_{tpk[p]}$ is a noise term, distributed according to a normal function, with expected value 0 and variance σ^2.

Table 1. Model specifications to assess effects of human encroachment, primary productivity, and daily maximum ambient temperature on diel activity rhythms (based on hourly movement rates) of 139 brown bears from six populations in Europe and North America (2004–2022).

Model no.	Model formula	Description
1	$\lambda^{*}_{tp} = \lambda_{hp}$	Diel activity depends on the hour of the day *h* and the population *p*, (λ_{hp}). The interaction of the time of day effect with season *s* and the addition of the random effect of the year ($\xi_{a[p]}$) are tested
2	$\lambda^{*}_{tp} = \lambda_{hps}$	
3	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]}$	
4	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{1} \cdot x_{1tk[p]}$	Diel activity depends on the hour of the day, the population, and the season (λ_{hps}). Activity also depends on the continuous effect of human encroachment ($\beta_{1} \cdot x_{1tk[p]}$), or primary productivity ($\beta_{2} \cdot x_{2tk[p]}$), or maximum temperature ($\beta_{3} \cdot x_{3tk[p]}$). These do not change across hours, populations, and seasons
5	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{2} \cdot x_{2tk[p]}$	
6	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{3} \cdot x_{3tk[p]}$	
7	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{1hp} \cdot x_{1tk[p]}$	Diel activity depends on the hour of the day, the population, and the season (λ_{hps}). Activity also depends on the continuous effect of human encroachment ($\beta_{1hp} \cdot x_{1tk[p]}$), or primary productivity ($\beta_{2hp} \cdot x_{2tk[p]}$), or maximum temperature ($\beta_{3hp} \cdot x_{3tk[p]}$). These change across hours and populations. The interaction with season is tested
8	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{2hp} \cdot x_{2tk[p]}$	
9	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{3hp} \cdot x_{3tk[p]}$	
10	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{1hps} \cdot x_{1tk[p]}$	
11	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{2hps} \cdot x_{2tk[p]}$	
12	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{3hps} \cdot x_{3tk[p]}$	
13	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{1hps} \cdot x_{1tk[p]} + \beta_{2hps} \cdot x_{2tk[p]}$	Diel activity depends on the hour of the day, the population, and the season (λ_{hps}). Activity also depends on the joint effects of human encroachment ($\beta_{1hps} \cdot x_{1tk[p]}$), primary productivity ($\beta_{2hps} \cdot x_{2tk[p]}$), and maximum temperature ($\beta_{3hps} \cdot x_{3tk[p]}$). These change across hours, populations, and seasons
14	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{2hps} \cdot x_{2tk[p]} + \beta_{3hps} \cdot x_{3tk[p]}$	
15	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{1hps} \cdot x_{1tk[p]} + \beta_{3hps} \cdot x_{3tk[p]}$	
16	$\lambda^{*}_{tp} = \lambda_{hps} + \xi_{a[p]} + \beta_{1hps} \cdot x_{1tk[p]} + \beta_{2hps} \cdot x_{2tk[p]} + \beta_{3hps} \cdot x_{3tk[p]}$	

We modeled the term λ_h, representing the effect of hour of the day in λ^*_{tp} (Table 1), according to a multivariate normal distribution with expected value a vector 0 of dimension equal to 24, and symmetric covariance matrix Σ. To account for the cyclical and autocorrelated nature of diel activity, the correlation between activity values at different hours of the day was considered in the covariance matrix. Specifically, we assumed that longer time periods between two observations would imply lower correlation between the corresponding activity values. Thus, each element (h, h′) of the 24 × 24 covariance matrix for h, h′ = 1, …, 24 and h ≠ h′, representing two hours of the same day or of consecutive days, was modeled as follows:

$$\exp\left(-\nu \cdot \min\left(\left|h-h'\right|, 24-\left|h-h'\right|\right)\right)/\psi, \tag{2}$$

where $\min(|h - h'|, 24 - |h - h'|)$ is the circular distance in time. This structure resolves a key challenge in estimation of activity patterns, which rarely accounts for autocorrelation of activity metrics (Donatelli et al. 2022). We modeled diagonal elements, representing the variance associated with the parameter distribution in each hour of the day, as $1/\psi$. Priors of model parameters are in the Supporting information.

To address the inherent complexity of the models and reduce computational time, we built increasingly complex models by adding terms and interactions to the best performing simpler models, thus avoiding fitting every possible combination of terms and interactions among variables. We used a three-step strategy for model fitting. First, we developed base models without the effects of environmental covariates (models 1–3, Table 1). In model 1, activity depends solely on the hour of the day and the bear population. In model 2, we tested the interaction of the hour of the day effect λ_h with season s. In model 3, we evaluated the inclusion of a random effect of year nested in population to account for the residual variance given by the difference in sampling periods among individuals in each population, i.e. $\xi_{a[p]}$. This is distributed according to the normal function $N(0, \mu^2)$, where 0 is the expected value and μ^2 the variance. Second, we used the best-supported among models 1–3 as a basis for more complex models to separately assess the effects of human encroachment ($x_{1tk[p]}$), primary productivity ($x_{2tk[p]}$), and daily maximum temperature ($x_{3tk[p]}$). For each of these variables, we also tested interactions with hour of the day, bear population, and season (models 4–12, Table 1). Third, we used the best-performing among models 4–12 to implement multi-effects models (models 13–16, Table 1), including the full model (model 16, Table 1). The latter modeled activity as a function of hour of the day, bear population, and season, in addition to human encroachment, primary productivity, and maximum temperature, whose effects may vary hourly, seasonally, and by population.

Model selection and validation

We ran two Hamiltonian Monte Carlo chains (Brooks et al. 2011) to generate posterior samples for each model. We visually assessed the convergence of chains using R packages 'MCMCvis' (www.r-project.org, Youngflesh et al. 2023) and 'coda' (Plummer et al. 2024). Chains were run for 5000 iterations with a thin of two to reduce autocorrelation in the sample, including a warm-up of 1000 iterations. From the posterior sample of 4000 values (each chain produced a sample of 2000, which we combined into one), we calculated the mean and 95% credible intervals of each relevant parameter.

We used R package 'loo' (Vehtari et al. 2024) to calculate the widely applicable information criterion (WAIC) index (Watanabe 2013) and compare the predictive performance of each model. Model selection is usually based on a difference of 10 WAIC (i.e. $\Delta\text{WAIC} \geq 10$) between models, with the lower score indicating a superior predictive performance (Burnham and Anderson 2002). Accordingly, we used the distribution of the difference in WAIC scores to account for sampling variability. Thus, if the range of values of $\Delta\text{WAIC} \pm 2 \cdot \text{SE}$ (the variability in the ΔWAIC is assumed to be normally distributed) included scores < 10, we regarded the difference in the predictive performance of those models as non-significant (Burnham and Anderson 2002).

Results

Among base models (models 1–3, Table 1), model 3, including the hour of day effect interacting with population and season, and the random effect of the year, was selected by WAIC (Supporting information) and used to construct increasingly complex models. Among single-effect models (models 4–12, Table 1), models 10, 11, and 12, including, respectively, the effect of human encroachment, primary productivity, and maximum temperature in interaction with hour of the day, population, and season, were selected by WAIC (Supporting information) and used to construct multi-effects models. The full (model 16, Table 1), including all aforementioned effects, was selected as the best performing model among all (Supporting information). Accordingly, all brown bear populations displayed a bimodal pattern of activity with peaks approximately aligned with the morning and evening crepuscular periods (Fig. 3). During summer, all populations showed higher crepuscular and nocturnal activity, and slightly lower diurnal activity, compared with the other seasons (Supporting information). Although activity rhythms were similar across populations, bears at northern latitudes (Karelia and Scandinavia) generally displayed higher activity levels, distributed in various diel phases (i.e. diurnal, crepuscular, and nocturnal hours), compared with the other populations (Supporting information). As expected from our prediction (P1), Yellowstone bears exhibited higher crepuscular and, to a lesser degree, diurnal activity, and slightly lower nocturnal activity compared with most European populations, especially those at southern latitudes (Apennine and Dinaric Pindos bears; Supporting information).

The effect of increasing daylength on bear activity rhythms differed between European and Yellowstone bears (Supporting information). European bears increased

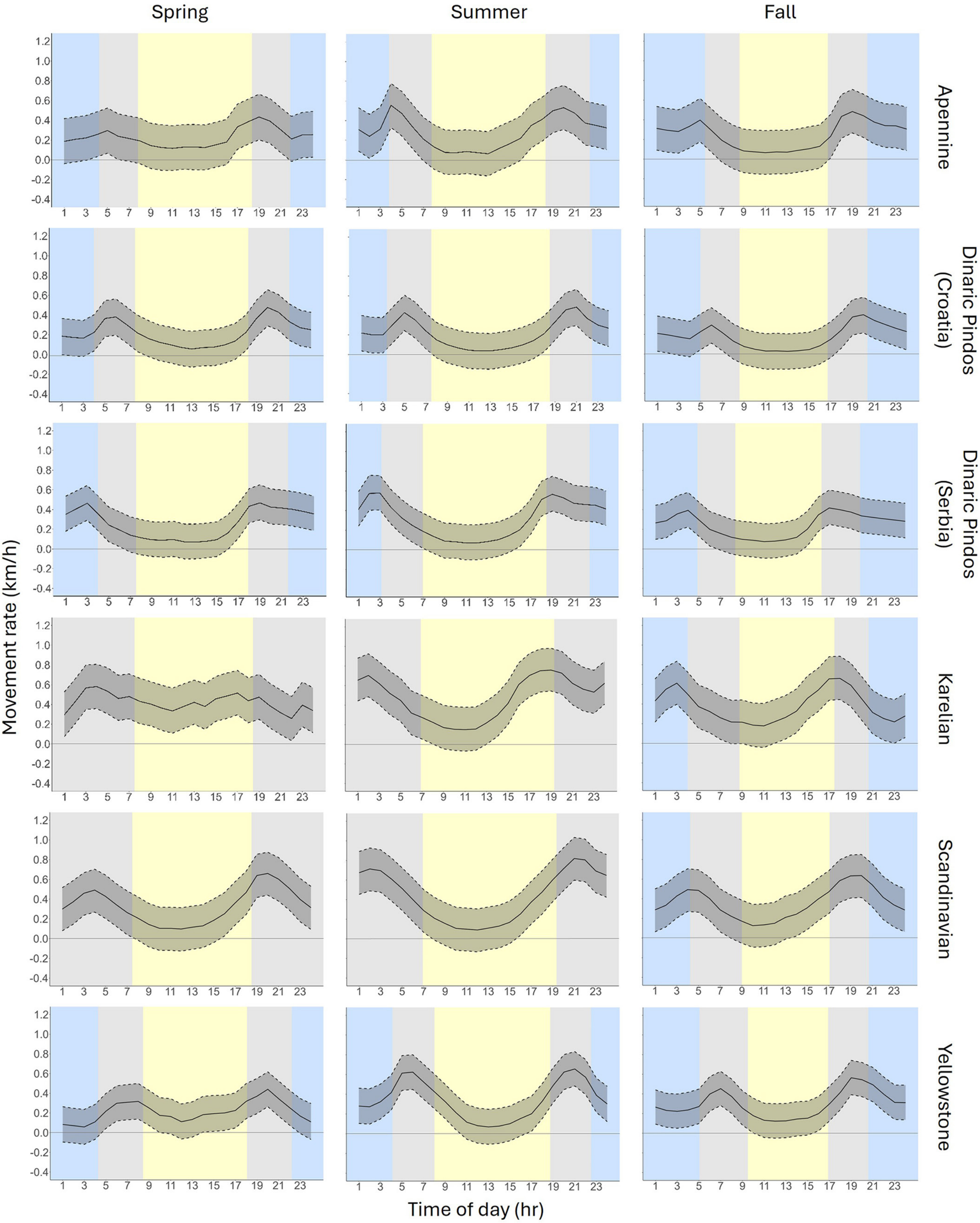

Figure 3. Seasonal diel activity patterns based on hourly movement rates (dashed lines: 95% credible intervals) of brown bears from six populations across Europe and North America (2004–2022). Based on sun altitude on the horizon (diurnal: sun altitude > 18°, crepuscular: sun altitude > −18° and < 18°, nocturnal: sun altitude < −18°), seasonally averaged diel phases are depicted by colored vertical areas (diurnal: yellow, crepuscular: gray, nocturnal: blue). Activity patterns were estimated with average daylength, global human modification index (GHM), normalized difference vegetation index (NDVI), and maximum temperature in each study area and season.

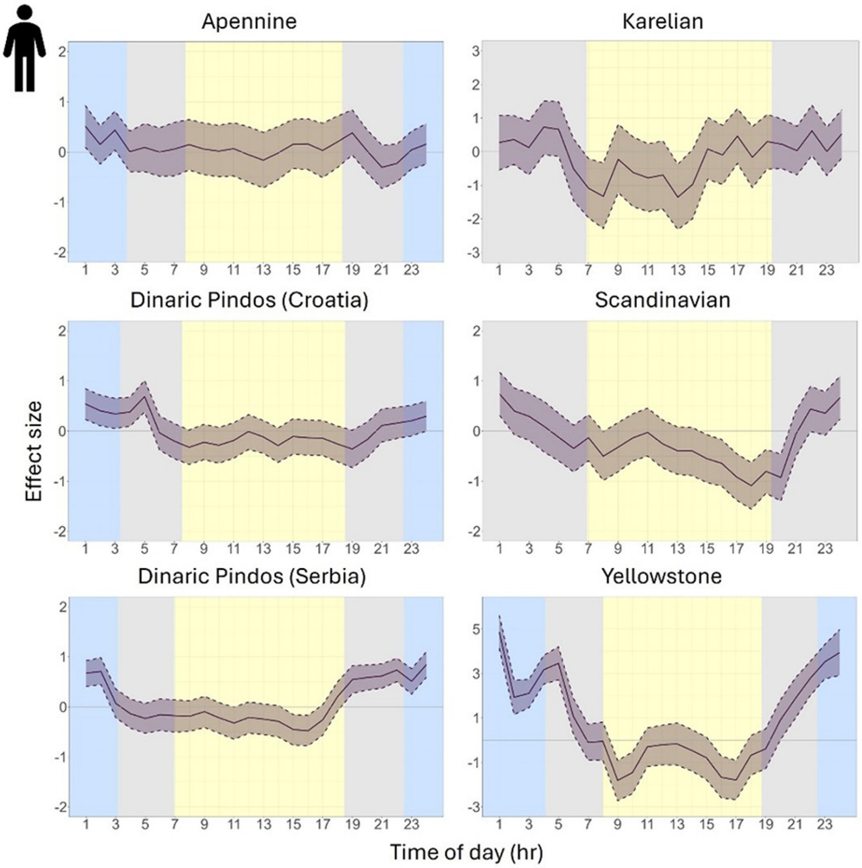

Figure 4. Predicted effects of the global human modification index (GHM) on diel activity patterns (based on hourly movement rates) of six brown bear populations from Europe and North America (2004–2022) during summer (dashed lines: 95% credible intervals). Diurnal, crepuscular, and nocturnal hours are depicted, respectively, by yellow, gray, and blue vertical areas (Figure 3). Negative and positive values of the effect sizes respectively represent the magnitude (β_1, c.f. Table 1) of decrease and increase in activity (km/h) in response to higher GHM values. Note the scale difference in the panels of Karelian and Yellowstone populations. For effect sizes during all three seasons see the Supporting information.

activity during darker hours at increasing daylength, whereas Yellowstone bears increased activity during light hours and reduced activity during darker hours. This indicates that factors beyond daylength may influence behavior differently in these regions. Analyzing daylength effects by periods of increase and decrease in daylight could clarify this pattern, but is outside the scope of this study (i.e. we included daylength in the models to account for latitudinal variations in daylight).

The effects of the global human modification of terrestrial systems (GHM), normalized difference vegetation index (NDVI), and maximum daily temperature on activity patterns of bears varied among populations and were modulated by both the hour of the day and the season. In all bear populations, higher GHM values were generally associated with a shift from diurnal to nocturnal and crepuscular activity (Fig. 4, Supporting information). The magnitude of the GHM effect was strongest for Karelian bears during spring and for Yellowstone bears during summer and fall, contrary to our prediction (P2) (Fig. 4; Supporting information).

As expected from our prediction (P3), we found that bear activity rhythms during hyperphagia were related to primary productivity depending on predominant feeding patterns. Namely, in hyperphagic Dinaric Pindos and Apennine bears relying on hard mast, higher NDVI values were related to a decrease in nocturnal activity and a slight increase in crepuscular activity, whereas hyperphagic Karelian and Scandinavian bears relying on berries displayed lower activity at higher NDVI values across all three diel phases, i.e. diurnal, crepuscular, and nocturnal periods (Fig. 5). Instead, Yellowstone bear activity patterns did not show a strong association with NDVI, and credible intervals overlapped zero on most hours (Fig. 5).

Contrary to our (P4), all European brown bear populations showed marginally decreasing diurnal and crepuscular activity with higher summer maximum temperatures, prompting a decrease in overall diel activity levels (Fig. 6). Conversely, Yellowstone bears exhibited a reduction in diurnal activity and a prominent increase in nocturnal and crepuscular activity with higher summer temperatures (Fig. 6).

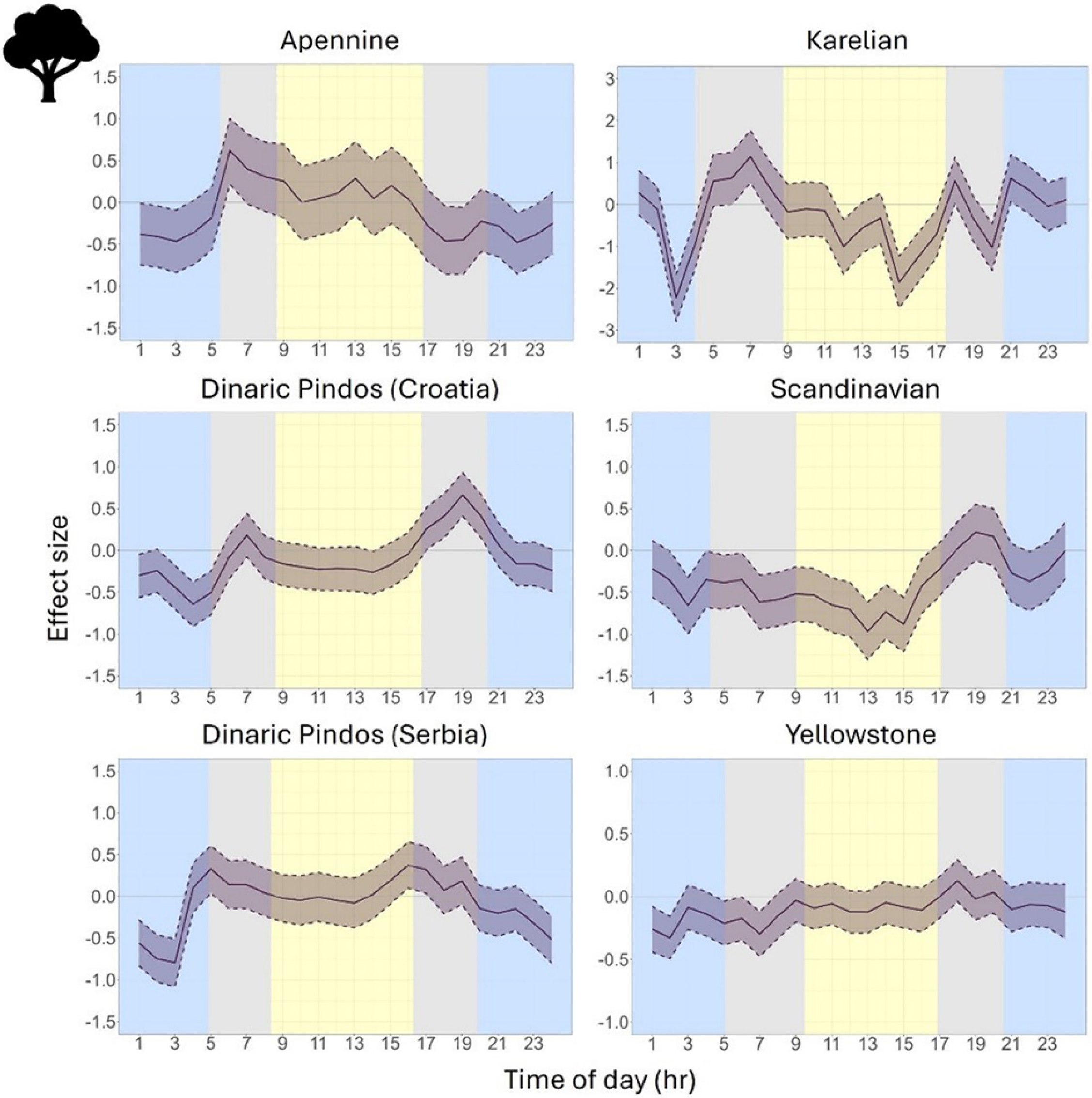

Figure 5. Predicted effects of the normalized difference vegetation index (NDVI) on diel activity patterns (based on hourly movement rates) of six brown bear populations from Europe and North America (2004–2022) during fall (dashed lines: 95% credible intervals). Diurnal, crepuscular, and nocturnal hours are depicted, respectively, by yellow, gray, and blue vertical areas (Figure 3). Negative and positive values of the effect sizes respectively represent the magnitude (β_2, c.f. Table 1) of decrease and increase in activity (km/h) in response to higher NDVI values. Note the scale difference in the panels of Karelian and Yellowstone populations. For effect sizes during all three seasons see the Supporting information.

Discussion

By examining the effects of human encroachment, primary productivity, and maximum ambient temperature, we gained insights into how these factors influence diel activity of brown bears globally, shedding light on the adaptive responses of the species to varying ecological contexts. We found that all bear populations analyzed displayed a bimodal and largely crepuscular activity pattern, as measured using hourly movement rates, in accordance with findings from previous studies (Schwartz et al. 2010, Ordiz et al. 2014, Bogdanović et al. 2021, Vicedo et al. 2023). The consistency of this bimodal pattern, despite the different ecological and management conditions of the studied bear populations, may be attributed to the predominance of endogenous mechanisms regulating circadian rhythms of both physiological and behavioral processes in brown bears (Ware et al. 2012, Rattenborg et al. 2017, Thiel et al. 2022). Nevertheless, in accordance with our prediction (P1), Yellowstone bears were less nocturnal, and more crepuscular and diurnal compared with European bear populations, especially at southern latitudes, where human encroachment is higher (Fig. 2). This result supports the key role that temporal segregation from humans may play for brown bears in the highly modified landscapes of Europe to

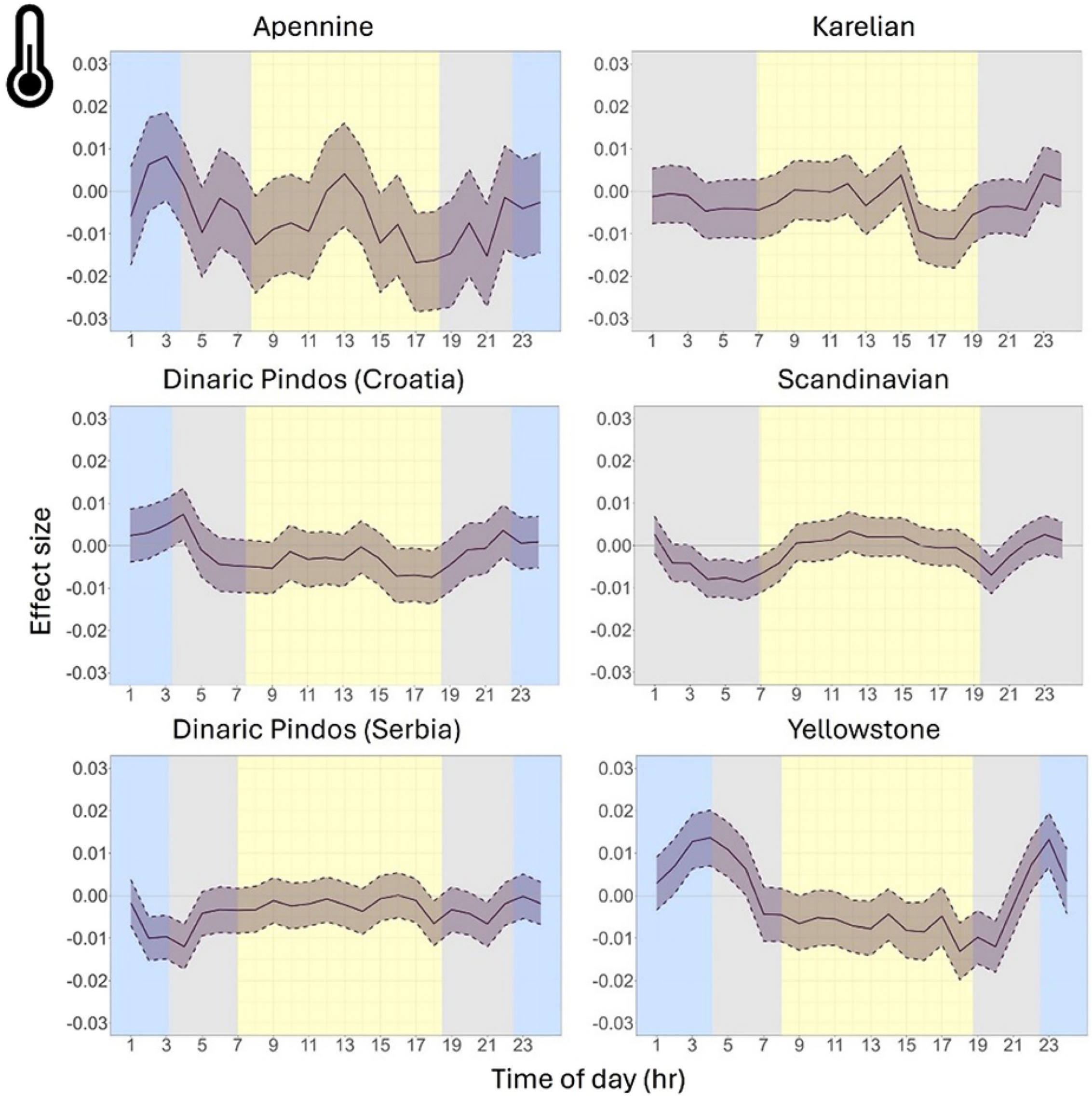

Figure 6. Predicted effects of maximum ambient temperature on diel activity patterns (based on hourly movement rates) of six brown bear populations from Europe and North America (2004–2022) during summer (dashed lines: 95% credible intervals). Diurnal, crepuscular, and nocturnal hours are depicted, respectively, by yellow, gray, and blue vertical areas (Fig. 3). Negative and positive values of the effect sizes respectively represent the magnitude (β_3, c.f. Table 1) of decrease and increase in activity (km/h) in response to higher maximum temperatures. For effect sizes during all three seasons see the Supporting information.

avoid direct contact with humans (Morales-González et al. 2020, Ordiz et al. 2021).

Pristine landscapes allow greater plasticity of activity patterns

In accordance with previous research (Ordiz et al. 2014, Gaynor et al. 2018), we found an overall increase of nocturnal and decrease in diurnal activity in all bear populations associated with greater human encroachment. However, contrary to our expectation (P2), we found that Yellowstone bears exhibited the strongest shift to nocturnality in response to human encroachment, specifically during summer and fall, when visitation rates are usually highest (National Park Service 2024). Although Yellowstone bears displayed greater crepuscular activity compared with European bears, it is unlikely that a possible higher temporal overlap with human activity in the largely unaltered landscape of Yellowstone prompted the strong increase in nocturnality we recorded. Instead, baseline activity of Yellowstone bears may be less constrained by human encroachment and, thus, able to display a more flexible response towards anthropogenic cues through more intense modifications, such as increased nocturnality. Conversely, activity patterns of European bears are already adapted to high levels of human encroachment through increased nocturnal activity at the expense of diurnal and crepuscular activity, particularly in southern Europe

(Kaczensky et al. 2006, Ordiz et al. 2014). Thus, although specific events (e.g. start of the hunting season [Ordiz et al. 2012] or human encounters [Ordiz et al. 2013]) may trigger an immediate modification in activity rhythms, a more extreme shift towards nocturnality may not be sustained for long periods (e.g. months), without implications for fitness.

We found that Karelian bears in spring exhibited a prominent increase in nocturnality in response to human encroachment, similar to Yellowstone bears in summer and fall. We also recorded that Karelian bears displayed greater diurnal activity during spring compared with the other seasons (Supporting information). This pronounced diurnality may be facilitated by the low anthropogenic encroachment experienced by Karelian bears in spring (Supporting information). The selected GHM values during spring were also generally lower when compared with the distribution of values experienced by Scandinavian bears in all seasons (Supporting information). This indicates that in areas of Europe where human encroachment is relatively low, i.e. comparable to Yellowstone, bears may be able to exhibit a more diurnal pattern of activity and, consequently, higher plasticity in their activity rhythms.

Anthropogenic risks and feeding habits modulate the spatio-temporal organization of activity during hyperphagia

In accordance with our prediction (P3), the relationship between primary productivity and European bear activity depended on key food sources during hyperphagia. Hyperphagic bears in southern Europe are dependent on hard mast (Bojarska and Selva 2012), which has been associated with higher NDVI values (Wang et al. 2004, Pérez-Girón et al. 2022). In contrast, hyperphagic bears at northern latitudes feed on berries, which can generally be found in more open habitats, such as early successional forests or clearcuts, characterized by lower NDVI values (Nielsen et al. 2004, Hertel et al. 2016a; Souliere et al. 2020). Accordingly, we found that increased bear activity during hours when bears were most active (i.e. around 05:00 and 19:00 in Apennine bears, 06:00 and 20:00 in Croatian bears, 03:00 and 18:00 in Karelian bears, 04:00 and 20:00 in Scandinavian bears, 04:00 and 17:00 in Serbian bears) was generally associated with higher and lower NDVI, respectively, in European bears at southern (Apennine and Dinaric Pindos bears) and northern (Karelian and Scandinavian bears) latitudes. Foraging during crepuscular hours may represent a time allocation strategy that lowers the risk of human encounters while optimizing foraging efficiency, that could partially be related to visibility during light hours (Hertel et al. 2016b). Accordingly, previous studies have hypothesized about the importance of sight for the feeding performance of brown bears, especially in relation to spotting berry clusters and higher efficiency of intake rates (Welch et al. 1997, Ordiz et al. 2012).

We observed a decrease in activity of Dinaric Pindos bears in areas of higher NDVI during nocturnal hours. Because NDVI may also reflect the amount of vegetational cover (i.e. lower NDVI values typically characterize more fragmented forests; Pettorelli et al. 2005, Steyaert et al. 2011), the aforementioned effect of NDVI on nocturnal activity may reflect Dinaric Pindos bears visiting open areas and supplemental feeding sites during times of day when human activity is lower (Fležar et al. 2019). A similar consideration may be true for Karelian bears using supplemental feeding sites predominantly during crepuscular and nocturnal hours (Penteriani et al. 2021). We additionally found that, during hyperphagia, Karelian and Scandinavian bears decreased their diurnal activity in areas characterized by higher NDVI. In response to hunting pressure, bears may find refuge in dense vegetation for diurnal resting (Ordiz et al. 2011, Steyaert et al. 2011). Whereas bears in Croatia are only hunted at supplemental feeding sites, in Karelia and Scandinavia they are hunted with baying dogs (Bischof et al. 2008, Le Grand et al. 2019), and thus may be more likely to rest in denser spots during daytime.

Hyperphagic bears in Yellowstone displayed a marginal response to NDVI as evidenced by the credible intervals overlapping zero on most hours, disproving our prediction (P3) for this population. The decrease in whitebark pine *Pinus albicaulis* abundance since the early 2000s may have contributed to the low correlation between NDVI and bear activity, with bears relying on alternative foods when nuts are not available (Macfarlane et al. 2010, Costello et al. 2014).

Human encroachment may limit adaptation to increasing temperatures

We found only a marginal shift of activity patterns in response to maximum summer temperatures, thus our prediction (P4) was only partially supported. With higher summer temperatures, diel activity of Yellowstone bears displayed the most prominent increase in nocturnal and crepuscular activity at the expense of diurnal activity. This may represent a thermoregulation tactic to avoid heat stress during summer months (Speakman and Król 2010, Terrien et al. 2011). European populations reduced diurnal and crepuscular activity at higher summer temperatures, but did not compensate with greater nocturnal activity, thus prompting a reduction in overall diel activity levels, possibly impacting daily energy balance (Karasov 1992). In combination with our findings concerning the effect of human encroachment on bear activity, this possibly indicates diminished opportunities for European bears, or more generally bears living in human-modified landscapes, to shift towards greater nocturnality if needed, such as for optimal thermoregulation (Terrien et al. 2011). In light of the on-going and projected climate change (Bellard et al. 2012), our findings indicate that bears in highly modified landscapes, whose diel activity patterns are already constrained by human encroachment into greater nocturnality, may be less adaptable to increasing temperatures and possibly more at risk of hyperthermia (Levy et al. 2018, Penteriani et al. 2019). Although this is not conclusive evidence, previous studies did not reveal differences in average body mass, which could influence thermoregulation efficiency, among European and Yellowstone brown bears (Swenson et al. 2007, Cameron et al. 2020).

Additionally, Yellowstone bears did not experience the hottest temperatures across study areas, which could have prompted the more evident behavioral thermoregulation we uncovered. Thus, other factors, such as human encroachment, may be contributing to the differing effect of maximum temperature on European and Yellowstone bears.

Caveats

Modeling a linear effect of maximum temperature on bear activity assumes that the relationship is consistent across the whole range of temperatures. Yet, the response to maximum temperature is more realistically shaped by the thermal thresholds of the species (Terrien et al. 2011). This implies that activity may be influenced by temperature only when the latter reaches values outside of the species thermal comfort zone. It is thus possible that our results under- and over-estimate the temperature effect at high and low maximum temperatures, respectively. Still, our analyses highlight a difference in how bears in Yellowstone and in the European populations modify their activity rhythms when temperatures are typically at their highest during summer. Given the relevant implications in a scenario where the climate is warming, future research could further investigate this topic (Bellard et al. 2012). In addition, we recognize there are population-specific variables besides human encroachment, primary productivity, and temperature that may influence brown bear activity rhythms. These include management systems (e.g. hunted versus protected populations, or whether supplemental feeding is provided; Hertel et al. 2016b, Morales-González et al. 2020, Supporting information), sex and reproductive status of individuals (Steyaert et al. 2013, Bogdanović et al. 2021), among others, in addition to the expected inter-individual variability (Hertel et al. 2017). Although we could not explicitly include all these additional factors in our models, these differences are accounted for in the effect of bear population and bear ID.

Conclusions

By assessing differences in diel activity rhythms among brown bear populations from Europe and North America we evidenced the importance of temporal segregation from humans as a behavioral strategy in human-modified landscapes. Large carnivores in Europe have expanded their distribution as a result of conservation policies and societal changes that occurred during the second half of the 20th century (Chapron et al. 2014, Cimatti et al. 2021). However, the increase in ambient temperatures associated with climate change (Bellard et al. 2012) and the anthropization of natural areas (Ren et al. 2023) represent potential constraints to future conservation. Greater nocturnality has been recognized as an effective strategy for wildlife to both temporally segregate from, and thus coexist with humans (Gaynor et al. 2018, Cox et al. 2023), and avoid hyperthermia (Terrien et al. 2011, Levy et al. 2018). Indeed, behavioral plasticity of bears likely played a key role in the recovery of populations that were nearly eradicated in both continents, including several of the populations in our study (Ripple et al. 2014). However, our results indicate that European bear populations may be reaching a behavioral and physiological limit in their adaptive capacity to modify their diel activity, potentially constraining their ability to respond to the consequences of climate change and increasing human impacts on the species. A more pronounced shift towards nocturnality may generate a mismatch between activity patterns and rhythms of other physiological processes, anatomical adaptations that optimize activity during certain light conditions (i.e. eye structure), optimization of foraging strategies, and intra- and inter-specific relationships, with potential implications for fitness (Levy et al. 2018, Walker et al. 2019). Although difficult to quantify, a better understanding of the relationship between behavioral adaptive capacity of bears' diel activity patterns and individual fitness, measured as longevity, fat reserves before hibernation, reproductive output, and ability to find mates, could help to assess the possible demographic implications for the modifications in brown bear activity patterns that we recorded (Ware et al. 2012, Fortin et al. 2013).

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Author contributions

Aurora Donatelli: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (equal); Writing – original draft (lead); Writing – review and editing (equal). **Duško Ćirović**: Data curation (equal); Writing – review and editing (equal). **Mark A. Haroldson**: Data curation (equal); Writing – review and editing (equal). **Đuro Huber**: Data curation (equal); Writing – review and editing (equal). **Jonas Kindberg**: Data curation (equal); Writing – review and editing (equal). **Ilpo Kojola**: Data curation (equal); Writing – review and editing (equal). **Josip Kusak**: Data curation (equal); Writing – review and editing (equal). **Gianluca Mastrantonio**: Formal analysis (supporting); Investigation (supporting);

Methodology (equal); Supervision (supporting); Writing – review and editing (equal). **Andrés Ordiz**: Supervision (supporting); Writing – review and editing (equal). **Slaven Reljić**: Data curation (equal); Writing – review and editing (equal). **Luca Santini**: Formal analysis (supporting); Investigation (supporting); Writing – review and editing (equal). **Frank T. van Manen**: Data curation (equal); Writing – review and editing (equal). **Paolo Ciucci**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Project administration (equal); Supervision (lead); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/ecog.07979.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.d51c5b0fd (Donatelli et al. 2025).

Code for the best selected model is available from Github: https://github.com/auroradonatelli/DielActivityRhythms.

Supporting information

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

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