

# Bridging human mobility to animal activity:

When humans are away, bears will play

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## ABSTRACT

In the Anthropocene, findings on animal behavioral flexibility in response to anthropogenic changes are accumulating: human presence and activity affect the distribution, movement, activity rhythm, physiology, and diet of animal species. However, conclusions are limited by the lack of simultaneous quantitative data on both the animal and human side. Hence, the dynamic link between animal behavior and human activity and mobility is often poorly estimated. Based on long-term monitoring of a wild bear population in the Trentino region (10 bears monitored from 2006 to 2019; 20 bear-years) combined with human mobility data (Cumulative Outdoor activity Index, derived from the Strava Global Heatmap) and tourist count records, we investigated how spatial behavior and activity rhythms of bears change with variations in experienced human disturbance. We found that bears were mainly nocturnal and that, on an annual scale, nocturnality was associated with movement behavior, but both were independent of experienced human disturbance. Furthermore, nocturnality tended to increase in periods of more intense exploitation of outdoor areas by humans. Overall, these preliminary findings show that bears exhibit a notable behavioral flexibility to minimize their exposure to human presence. Through the application of different sources of human activity data, this work showcases that the integration of high resolution animal movement data with dynamic data on human mobility is crucial to meaningfully catch wildlife responses to anthropisation.

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## CCS CONCEPTS

- Applied computing → Life sciences → Computational biology;
- General and reference → Cross-computing tools and techniques → Empirical studies

## KEYWORDS

Human mobility, Nocturnality, Outdoor recreational activity, Strava-derived Cumulated Outdoor activity Index, Spatio-temporal risk avoidance, *Ursus arctos*

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## 1 Introduction

Space is a shared but finite resource. The way a species moves and exploits an environment thus depends on how other species might move and exploit it too. This is particularly relevant in the context of a prey-predator interaction (1): the predator seeks to locate the areas exploited by the prey, while the prey moves within a landscape of fear, fleeing from the predator either because of a proactive or reactive behavior (2). As a result, predators affect the demography of their prey both directly, through consumptive predation, and indirectly, through antipredator behaviors costs that preys have to sustain to minimize predation (3).

Over the past 200 years, humans have become the dominant predator across many ecosystems (4), even of large terrestrial carnivores (5), setting themselves as the main source of fear for many wild species (6). Along with an unsustainable predatory behavior (4), human populations have also increased their land-coverage (7), affecting the space-use strategy (8) and activity rhythm (9) of several animal populations.

Behavioral flexibility may help animals cope with anthropogenic disturbance (10), changing the classical understanding on the biology of many species we have built upon so far (11). For instance, many known migratory species tend to modify their migratory behavior in response to current environmental changes and may even become resident in a near future (12, 13).

In the Central Alps, an isolated brown bear (*Ursus arctos*) population has recently re-established in a highly anthropic area (14) where mountaineering and other outdoor activities are commonly practiced, although with varying intensity across seasons. In this anthropogenic context, bears spatially respond to human disturbance by exploiting those areas which are less disturbed (15, 16). It is less clear whether bears also temporally adjust their behavior to couple with human disturbance, e.g. shifting towards nocturnality as observed for several species living near human settlements (9).

In this study, we fill this gap by integrating animal movement ecology and human mobility science (17) to examine the spatiotemporal behavioral flexibility of the Alpine brown bear population in response to the intensity of human disturbance. We determined human disturbance by relying on two different sources of information: Strava, an application that tracks users during outdoor activities (traditionally runners, hikers, or bikers), and tourist count data. From the former, we determined an index reflecting the volume of human activity in a given area (Cumulative Outdoor activity Index; 16), which is spatially accurate (20x20 m) but temporally static (i.e., the index does not change over the period of the study). The latter reflects seasonal trends in tourism in the region of the Central Eastern Alps where this work has been performed, which are temporally dynamic (monthly values), but summarized across space.

We conducted a series of analyses at different spatiotemporal scales to relate these two indexes of human disturbance to two metrics depicting bear behavior, i.e. diurnality (the propensity of an animal to be active during daily hours with respect to night ones; 9) and daily movement length (i.e. cumulative sum of step lengths measured between consecutive locations within a day). First (Q1), we investigated whether the individual annual (intended as the period March-November, when bears are not hibernating) diurnality and movement of bears varied in function of spatial heterogeneity in human disturbance, expressed by an annual index of human disturbance derived from the COI. We also explored correlations between these two metrics of bear behavior, to assess whether bears exhibit a behavioral syndrome in response to anthropogenic pressure (18). We expected that bears exposed to lower human disturbance should exhibit an average higher annual level of diurnality (9) and should move more (8). As a consequence, we also expected a positive correlation between annual average diurnality levels and daily movement length. Then (Q2), we introduced a more dynamic component of human mobility in our assessment, i.e. monthly count data of tourists, to compare their trend with those of bear diurnality. We performed this analysis at the same temporal scale, controlling for daily temperature, with the expectation to detect a

higher nocturnality in bears during the highest peaks of the tourism season.

## 2 Material And Methods

### 2.1 Study site and animal tracking data

The study was carried out in the Autonomous Province of Trento, Italy, a mountainous region located in the Central Eastern Alps (Figure 1). The study area consists of low, wide valleys surrounded by mountain ranges that soar above 3,000 meters. Human settlements and infrastructures are most prevalent at lower elevations, whereas dense forest covers the lowest portions of mountainous reliefs, grasslands dominate at higher elevations, and barren ground or glaciers cover the highest portions. There is a diverse community of large mammals, including roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), gray wolf (*Canis lupus*), and brown bear. The latter was on the brink of extinction in the late 1990s until recovering thanks to a EU co-funded reintroduction project that relocated 10 bears from the neighboring Dinaric Alps (19). Since then, the population has increased and presently numbers about 100 bears (20). However, the population faces obstacles that could still prevent its long-term conservation, such as a lack of landscape connectivity (15), a relatively high rate of human-caused mortality (~60% of adult bears; 21), and loss of genetic variability (22).

As part of the monitoring programme implemented after the reintroduction project, between 2006 and 2019 some individuals were captured and tracked using telemetry technology (Vectronic GPS-GSM collars, Vectronic Aerospace GmbH, Berlin, Germany). A bi-axial accelerometer, which was integrated into the Vectronic GPS-GSM collar, was also fitted to some individuals to track their activity levels. We considered for these analyses only those bears equipped with a GPS and an accelerometer. To improve data quality, we removed duplicated locations and those considered unreliable (i.e., from impossible movement, outside the study area, and with very low accuracy). We limited our analyses to the period between March 15<sup>th</sup> to November 15<sup>th</sup> to avoid any possible bias due to animal winter hibernation. We resampled the trajectory to a maximum of one location every 30 minutes ( $\pm 5$  min tolerance) and subset it by only taking into account telemetry monitoring periods longer than 30 days and consisting of at least 100 locations. In total, we considered for the analysis 20 bear-year paths from 10 individuals (7 females, 3 males).

### 2.2 Human mobility data

**2.2.1 Strava data.** Strava (San Francisco, CA, USA) is a proprietary tracker service enabling users to register their paths from personal tracking devices, such as smartwatches, mobile phones, and bike computers. Using the Strava Global Heatmap, a visualization of the cumulative outdoor activity tracks recorded

by users, we derived the Cumulative Outdoor activity Index (COI). This newly-developed index, ranging from 0 (no outdoor activity in the 20x20-m cell) to 1 (very high outdoor activity in the cell), is a single static representation of all aggregated, public activities uploaded to the Strava App. Importantly, the spatial patterns in outdoor activities do not change across years (23), making the index an effective representation of the volume of human activity in a given area (see 16 for further details on data collection, processing, and validation). The spatial distribution of the COI at the study site is shown in Figure 1.

**2.2.2 Tourism count data.** Data on monthly tourism volume were retrieved from the Statistical Institute of the Province of Trento (ISPAT). We obtained the monthly number of nights tourists stayed in lodging facilities (e.g., hotel, bed and breakfast, private housing) from 2006 to 2019 (14 years). We used the total number of nights, rather than the total number of tourists, because it accounts for stay duration and was thus considered to be a more robust proxy of overall disturbance.

## 2.3 Statistical analysis

Data processing, analysis and plotting were computed using R software (v 4.2.1; 24). In particular, data processing was based on the *tidyr* and *dplyr* R packages (25, 26), while plotting was based on the *ggplot2* R package (27). Other packages that we used for specific modeling and statistical testing are reported in the respective subsections.

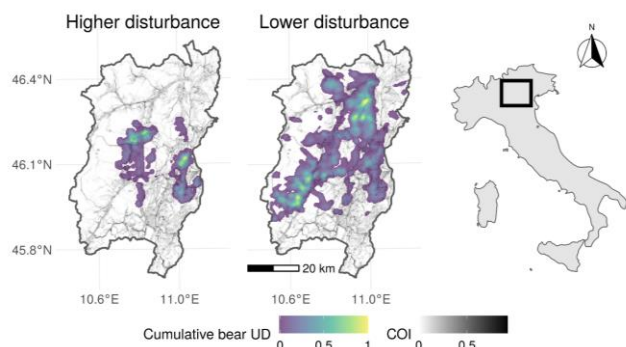


Figure 1: **The relative utilization distribution of bear-years ranging in areas with higher (left) vs. lower (center) human disturbance, as depicted by the Cumulated Outdoor activity Index (COI, gray scale in the background). The location of the study area within Italy is shown for reference (right).**

**2.3.1 Annual index of experienced human disturbance.** We quantified experienced human disturbance for each bear-year by measuring the Bhattacharyya (28)'s affinity index between the 95% annual utilization distribution (UD) of each bear-year and the COI distribution, hence accounting for surfacic and intensity overlap, and dividing it by the area of the 95% UD, to make it independent of the area size. The utilization distributions were estimated using kernels based on random Brownian bridges ("BRB.D" and "BRB" functions from the *adehabitat* R package, 29);

the diffusion coefficient was estimated first, smoothing was set at  $h_{\min} = 500$  meters, immobility was considered as a movement not exceeding 100 meters, and data independence was considered as soon as a time difference of more than 6.5 hours occurred. The higher the values of the Bhattacharyya index, the more heavily used by Strava users are the areas occupied by bears.

**2.3.2 Index of bear diurnality.** Activity data, as derived from bi-axial accelerometers (ranging from 0 to 255), were used to quantify the level of activity and diurnality of bears on each day. The activity level (along the  $x$  and  $y$  axes) accessible from the collars corresponds to a 5-min sampling, in which each measure is itself the average of a 5-sec activity sampling. We first summarized the activity along the two axes in one singular measure by taking the mean along the  $x$ - and  $y$ -axis. Then, as GPS and activity sampling rate differed, we matched activity to each GPS location by considering the average measure of activity within a 30-min window around GPS location acquisition time. We considered a mean value greater than 5 as non-resting time, which was then coded on a binary scale to denote active vs inactive behavior. The value of 5 was chosen because it matches with a break in the slope of the distribution of recorded activity values (from highly represented to less represented values). We then calculated an index of diurnality at the daily scale as  $ID = (d - n)/(d + n)$ , where  $d$  and  $n$  indicate the mean of the binary activity during the day and night, respectively. Specifically, each location was classified as 'daytime' when it occurred between sunrise and sunset, and 'nighttime' for all other times. The index ranges between -1 (fully nocturnal) to 1 (fully diurnal). For biological relevance, we did not consider Julian days, but consider as "a day" the 24-h time period starting from 7am. Lastly, we obtained the annual level of diurnality as the average daily index of diurnality, for any given bear-year.

### 2.3.3 Statistical testing

**Q1: Are annual levels of experienced human disturbance, diurnality, and daily movements associated?**

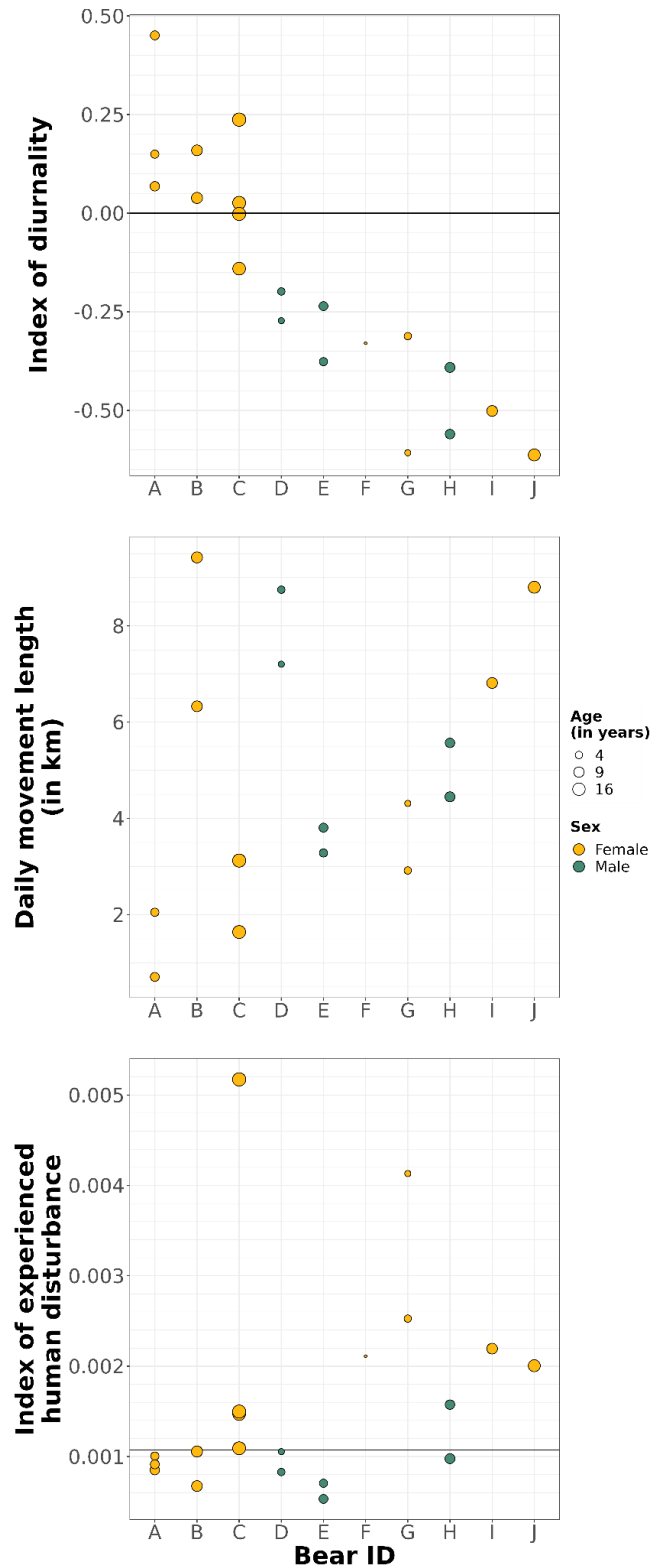
To assess whether we could identify behavioral syndromes in brown bears linking spatial behavior, activity patterns, and human disturbance, we built three Linear Mixed Models (LMM) considering, for each bear-year: (i) the average annual level of diurnality (ID) of bears as a function of the annual experienced index of human disturbance (HD), (ii) the square root of annual average bears' daily movement length (DML, in km) as a function of the annual experienced index of human disturbance, and (iii) the square root of annual average bears' daily movement length as a function of the average annual level of bears' diurnality. For daily movement length, we only considered days for which we had at least 5 locations, and bear-years for which we had at least 30 such days (16 out of 20 bear-years). In all models we controlled for sex as a fixed predictor, and considered the identity of the bear as a random effect on the intercept, using LMM fitted with the "lmer" function of the *lme4* R package (30). We obtained singular

p-values for each predictor by removing them one by one and comparing the likelihood of the models using the “drop1” function of the *base R* package. Before fitting, we checked that the predictors were symmetrically distributed to ensure a reliable fit. After fitting, we checked whether the necessary statistical assumptions were met (using the distribution of residuals, QQ-plots, and plots of the fitted values against the residuals), using the *DHARMA R* package (31). We also inspected the stability of the model on the basis of the Cook’s distance and *dfbetas* (*influence.ME R* package, 32). For the latter, we performed the analysis at the observation or random group level (i.e. evaluating the changes in estimates when removing one observation, or group of observations, at a time).

*Q2: Does bear diurnality change over the year, in relation to trends in tourism volume?*

To assess the trend in bear diurnality over the year, we used the daily indexes of diurnality (ID), which we scaled (i.e. to a mean of 0 and a standard deviation of 1) within each bear-year. The mean trend and associated 95% confidence interval were obtained by calculating a locally weighted scatterplot smoothing (loess, “loess” function in *base R* package; smoothing argument “span” set to 0.25). The same procedure was adopted to obtain the mean trends of bear activity. The seasonal pattern of human activity was instead approximated by the monthly count of tourists in Trentino (scaled within year), from 2006 to 2019, from which we extracted the average monthly count and the associated 95% confidence interval. Since temperature peaks in summer when tourists are expected to be most numerous, we controlled for a potential confounding seasonality effect. Under a heat-shield hypothesis, the bear diurnality level should relate to the maximum temperature experienced during the day. To this end, we modeled the daily index of diurnality as a function of the daily maximum temperature (i.e., the 95<sup>th</sup> percentile of the daily temperature recorded by an individual’s collar sensor), using a LMM as detailed above and considering year and month as random effects on the intercept. We observed no temporal auto-correlation issue (“check\_autocorrelation” function of the *performance R* package, 33). We thus calculated the marginal R-square of the model (accounting only for non-random factors) using the “r.squaredGLMM” function of the *MuMIn R* package (34).

Figure 2: Annual average diurnality level (upper panel), daily movement length (intermediate panel), and experienced human disturbance (lower panel) for each individual. Dots denote bear-years ( $n = 20$ ; for some years the average daily movement length could not be calculated, see Methods for details). The horizontal line indicates the threshold to consider diurnality vs. nocturnality (upper panel) or moderate vs. low human disturbance (lower panel). Age and sex are reported for reference.



### 3 Results

Bears were overall living in low to moderately disturbed areas (Figure 2, lower panel). Most of the bears (7 out of 10, 70%) were mostly nocturnal, and those mostly diurnal were females (Figure 2, upper panel). No clear differences in daily movement length (Figure 2, intermediate panel) were instead observed among bears of different cohorts (sex and age), yet the lowest values ( $< 2$  km) were those of females with cubs of the year.

*Q1 At the annual scale, bear diurnality and daily movement length are not related to human disturbance but most diurnal bears move less.*

Bear annual diurnality level was independent of the annual index of experienced human disturbance (LMM; est. = 7.01,  $CI_{2.5-97.5\%} = [-123.40, 86.40]$ ,  $\chi_1 = 0.03$ ,  $p = 0.87$ ; Figure 3A), as well as the sex of the bear (LMM, reference are females; est. = -0.13,  $CI_{2.5-97.5\%} = [-0.53, 0.28]$ ,  $\chi_1 = 0.395$ ,  $p = 0.55$ ), and so was it for daily movement length (LMM; effect of experienced human disturbance: est. = 280,  $CI_{2.5-97.5\%} = [-74, 596]$ ,  $\chi_1 = 1.22$ ,  $p = 0.29$ ; effect of sex, reference are females: est. = 0.40,  $CI_{2.5-97.5\%} = [-0.55, 1.36]$ ,  $\chi_1 = 0.35$ ,  $p = 0.58$ ; Figure 3A). However, bear annual diurnality level was negatively correlated with daily movement length (LMM; est. = -1.31,  $CI_{2.5-97.5\%} = [-2.18, -0.37]$ ,  $\chi_1 = 7.67$ ,  $p = 0.02$ ; Figure 3A, Figure 3B).

*Q2 Diurnality varies along the year, decreasing when the number of tourists is higher.*

Bear diurnality and tourist frequentation varied over the year following antiparallel trends (Figure 4). In particular, diurnality levels of bears decreased from June, concomitantly to a rise in tourist volume and an overall increment of activity rate. Diurnality reached its lowest level in July, close to the tourism peak, before slowing reincreasing when tourism, and overall daily activity, decreased during the second half of the year. Such a response anecdotally appeared stronger in individuals experiencing the highest disturbance (Figure 4, dark gray lines in the background). When controlling for environmental temperature, we observed that the daily index of diurnality was positively related to the maximum daily temperature experienced by the bear, but its effect size was negligible compared to the amplitude of variations in diurnality over the year (LMM; est. = 0.01,  $CI_{2.5-97.5\%} = [0.0001, 0.02]$ ,  $\chi_1 = 4.00$ ,  $p = 0.046$ ;  $R^2 = 0.002$ ).

### 4 Discussion

In the Anthropocene, unveiling the association between human disturbance and animal behavior is of uttermost importance to understand the impact of human presence and activity on wildlife behavior (35). In this work, we have been able to show the complexity of such a relationship in a context where brown bears and humans tightly coexist over the landscape. Through the implementation of different sources of human mobility data, we

demonstrated that both space use (Figure 1) and daily diurnality (Figure 4) patterns of this apex predator are affected by human activities, eventually suggesting that bears might consider humans as a threat (36, 37), in a landscape of fear framework (6).

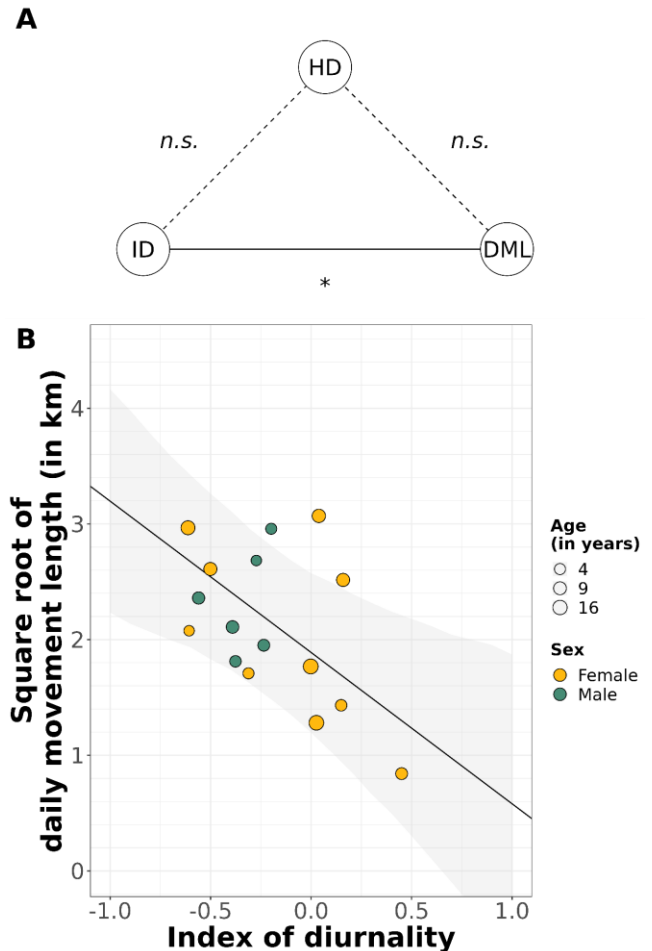


Figure 3: Association between annual experienced human disturbance, diurnality, and daily movement length for different bear-years. Panel A: No association between annual average diurnality (ID) and human disturbance (HD), nor between annual average daily movement length (DML) and human disturbance were observed. Instead, annual average diurnality was negatively associated with average daily movement length. Panel B: Predictive plot denoting the relationship between diurnality and daily movement length for each bear-year. The solid line and the light grey background depict the mean and 95% confidence interval of predicted values, respectively, when the effect of sex was averaged.

In our analyses, we firstly assessed the possible emergence of a behavioral syndrome in brown bears, putting in relation human disturbance with activity rhythms and space use tactics of these animals, at the annual scale (Figure 3). Our results

did not provide evidence of a clear behavioral syndrome in brown bears as observed for example in the Scandinavian bear population (18). Activity rhythm and daily movement length were however negatively correlated to one another but showing an opposite relationship than in the “spatio-temporal behavioral syndrome” evidenced in Scandinavian bears (18). This suggests that brown bears exposed to varying levels of human footprints (87 [Trentino] vs. 4–7 [south central Sweden] inhabitants/km<sup>2</sup>) apply different tactics when moving throughout the landscape, with an activity–exploration pattern likely depending on human presence (more nocturnal in Trentino, this study, and more diurnal in south central Sweden, 18).

The counterintuitive lack of a relationship at the range scale level between activity rhythms and human disturbance might be due to the Strava-based index of disturbance that we implemented for this analysis. Although COI is spatially accurate (20x20-m cell), it is temporally static, making it likely suboptimal for examining temporal responses of animals to changes in human mobility. To overcome this limitation, we extracted a temporally dynamic index of human disturbance, i.e. the monthly count of tourists visiting Trentino. The tourism count index does not directly measure outdoor activities, but as Trentino is a popular tourist destination for mountain enthusiasts, its correlation with an increase of outdoor activities is very likely. While this index is spatially coarser, its temporally dynamic properties allowed us to detect an anti-parallel trend between tourism seasonal patterns and bear diurnality, evidencing a clear behavioral response to human disturbance. Specifically, when tourism increased over the summer, bear diurnality decreased, despite an overall increment of activity levels. Since humans exploit the mountain as recreational areas at most during the day (39), it is therefore reasonable that bears switch their activity patterns towards nocturnality, to minimize the risk of encounters. Accordingly, direct encounter of humans by bears has been found to be generally associated with a shift towards being more nocturnal (40). Further, it has been observed that bears living in human-dominated areas tend to become more nocturnal (in comparison to bears living in wilderness areas), and that their survival rates increase when attaining nocturnal activity levels above 75% (41). In Trentino, where the frequency of human-bear encounters is relatively high (42), as well as the density of humans (87 inhabitants/km<sup>2</sup>) and infrastructures (density = 95 km/100 km<sup>2</sup>), it is very likely that human presence and activity exert a pressure on bears to be active at night. Therefore, it was unsurprising to find that the majority of bears were overall mainly nocturnal (as preliminary indicated by 39), analogously to their originate Dinaric conspecifics (43).

We acknowledge that the observed anti-parallel trends between human disturbance and bear nocturnality might have been driven by other intrinsic or extrinsic factors affecting bear behavior and physiology. For instance, the timing and intensity of bear daily activity may be affected by other changes in their seasonal cycle (such as post-hibernation, reproduction, or migration), energetic requirements (from hypophagia to

hyperphagia), availability of food (44), or maternal care due to the presence of cubs (45).

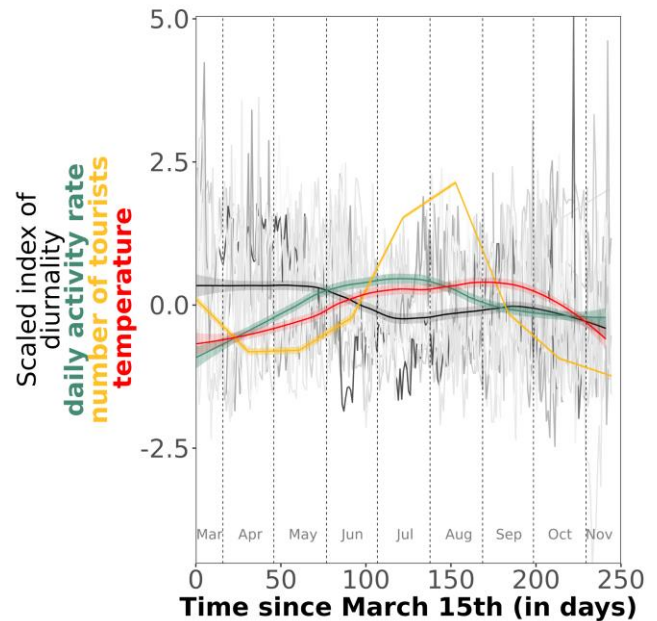


Figure 4: Patterns of bear diurnality, bear activity and touristic presence during the year (March - November). Diurnality daily indexes (scaled within individual-year) are depicted by the gray lines whose darkness is relative to the annual index of experienced human disturbance for any given bear-year (light gray = least disturbed, dark gray = most disturbed). The average diurnality curve (scaled within bear-year, with associated 95% CI, obtained using a loess with a smoothing span of 0.25) is indicated by the black solid line. Average activity level (scaled within bear-year, with associated 95% CI, similarly calculated) is depicted in green. Average temperature from bear collars (scaled within bear-year, with associated 95% CI, similarly calculated) is depicted in red. Average number of tourists (scaled within a year, with associated 95% CI) is depicted in yellow.

We could not account for several of these factors in our analyses, due to a combination of lack of information and limited sample size. However, we correlated the highest daily temperature with the daily level of nocturnality of the same animal, to assess the heat-shield hypothesis (i.e. thermal equilibrium is more easily met at night). The lack of any relevant correlation suggests that temperature is not the major driving factor of the observed changes in nocturnality that we observed. The temporal adjustment of activity patterns is likely to relate with changes in human pressure. This finds support in previous works that evidenced a physiological (46) and behavioral (36) response of bears to humans, with stress levels increasing in anthropized habitats.

Overall, these results clearly denote a response by bears to human disturbance, both in their space use tactics and in the allocation of their activity budget. Bears minimize their risk exposure by maximizing human avoidance when moving, with nighttime acting as a period of refuge from anthropogenic pressure (47). It is very likely that such a strategy involves cognitive capabilities, because remembering both the location (spatial memory, 48) and the timing of the risk (temporal memory) is essential for bears to move in a human-dominated landscape of fear. Memory has already been proved to be fundamental for bears foraging activities (49), as well as for other species with much contrasted biology (roe deer, 50; chimpanzees, 51) and for flexibly adjusting their activity rhythm to human presence (chimpanzees: 52, 53). Coupling spatio-temporal dynamicity of human disturbance with memory-mediated behavioral responses by wildlife remains a fertile terrain of research for a better understanding on the effects of anthropogenic impacts on animal behavior and, eventually, population fate.

## 5 Conclusion

This work contributes to understanding the complex interactions between wildlife and human behaviors, showing the clear necessity to couple high resolution dynamic data on both animal and human mobility, to derive meaningful ecological inference. We argue that the biggest challenge that ecologists and human mobility scientists need to face is related to the spatial mismatch between the areas where animals are tracked (i.e., in the wild) versus those where human mobility data is primarily collected (i.e., in cities). Typically, animals range in areas where the availability of human mobility data is rather limited, either because the human presence itself is limited or - and this is the worst case scenario - because collection of human mobility data is hampered by technological constraints (e.g., lack of a cover network to track people from the activity of their mobiles), privacy concerns (54), or a combination of both. In this study we showed that proxies for human disturbance in (relatively) remote areas can indeed be beneficial for assessing the impact of outdoor activities and tourism on wildlife. However, we feel that the integration of dynamic measures of human presence in animal movement studies is still in its pioneering stage. Beyond assessing the effect of anthropogenic pressure on animal behavior (as done for instead in our work), simultaneous monitoring of animal populations and human mobility (17) could aid in a better understanding of the dynamics of human-animal conflicts, e.g. zoonosis, crop raiding, and depredation on livestock. We therefore invoke a multidisciplinary common effort to integrate human mobility science with animal ecology.

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## ETHICAL STANDARDS

Brown bears are currently protected under European (Habitats Directive 92/43/EEC, incorporated in the Italian legislation via D.P.R. 357/97) and Italian Laws (L. 157/92), and included as a strictly protected species in the Bern Convention (1979). Under derogation of the aforementioned Habitat Directive, approved by the Italian Institute for Environmental Protection and Research (ISPRA), it is permitted to capture animals for research, public safety, and damage prevention purposes. Within these limits, all trapping and handling operations of brown bears are regulated by the "Interregional action plan for the conservation of the brown bear in the central-eastern Alps" (3), approved by Directorial Decree n. 1810 of 5 November 2008 and amended by Directorial Decree Protocol 0015137 PNM of 30 July 2015.

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