



## Research Article

## Spatial and temporal patterns of human avoidance by brown bears in a reintroduced population

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### Abstract

The preservation of large carnivores is a formidable challenge for biodiversity conservation in Europe, where few areas can be considered wilderness. In this context, brown bears *Ursus arctos* in Europe coexist with people in densely settled, multi-use landscapes and hence have to cope with diffuse human activities. This calls for robust knowledge on the effects that such activities have on brown bear distribution and behaviour. We sampled 220 km<sup>2</sup> with 60 camera trap locations over four consecutive years to investigate the effect of human activity and settlements on brown bear spatial and temporal patterns across the core area of the reintroduced population in the central Italian Alps. By using images of people and vehicles to quantify human activity at camera trap sites we could directly study how humans affect bears' activity and occupancy. We assessed bear's daily patterns and found a predominantly crepuscular and nocturnal behaviour, with peaks of activity before dawn and after dusk. We also modelled bear occurrence and detection probability around the dawn and dusk hours only, i.e., when the likelihood of encounters with humans was highest. Results showed that proximity to settlements and anthropogenic traffic, especially motorised, significantly and negatively influenced bear occupancy rates across the study area. Pedestrian and motorised traffic rates were both also negatively related to detection probability. By using four years of data and a refined modelling approach that considered the hours of maximum activity overlap of humans and bears, our results extend the findings from an initial study by suggesting that human presence induces not only temporal, but also spatial displacement. These findings are consistent with evidence from other populations that bears living in human-modified landscapes adapt their spatio-temporal patterns to avoid humans, an important prerequisite for the coexistence of bears and people in complex human-natural landscapes.

## Introduction

The preservation of large carnivores is a formidable challenge for biodiversity conservation (Chapron et al., 2014; Dorresteijn et al., 2014). This is especially true in Europe where, due to higher human population densities and increased habitat fragmentation and alteration (Zedrosser et al., 2011; Chapron et al., 2014), few areas can be considered wilderness (Linnell et al., 2001; Zedrosser et al., 2011). Despite this challenge, in recent decades carnivores have been making a comeback, largely due to re-colonization of historical ranges following the decline of traditional agricultural activities, abandonment of mountain areas by humans, forest restoration, ungulate recolonization and change of conservation policy (Breitenmoser, 1998; Peters et al., 2015). That is the case for the brown bear (*Ursus arctos*) that, although being historically persecuted, is now the most abundant large carnivore in Europe, with all population ranges being relatively stable or slightly expanding (Chapron et al., 2014; Lamb et al., 2020). However, success in carnivore recovery also increases conflict with humans (Linnell and Boitani, 2011). This calls for an improvement of our knowledge of the effects that human activity has on brown bear distribution and behaviour, especially in areas where wild populations are still vulnerable.

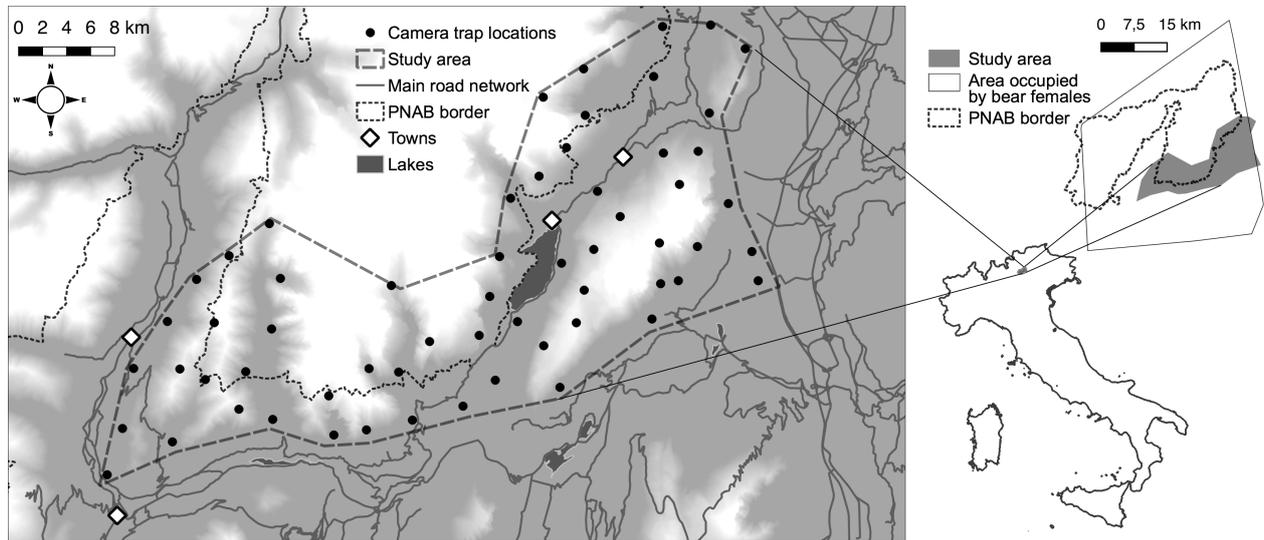
Anthropogenic activities, predominantly for recreation, are particularly common in bear habitats across Europe (Fortin et al., 2016), where forests are heavily managed by foresters and hunters and are

used by the general public mainly for hiking, camping and mountain biking (Kaczensky et al., 2006). Previous studies suggest that the primary mechanism by which human disturbance may impact brown bears is through temporal and spatial displacement (Kaczensky et al., 2006; Fortin et al., 2016). Studies in North America similarly documented how linear features (road/trails) networks influence grizzly bears by altering habitat availability and movement (Graham et al., 2010; Northrup et al., 2012). Interestingly, in addition to the presence of the linear features themselves, human activity along this network, such as motorised traffic, seemed to be a prominent driver of animal avoidance behaviour (Northrup et al., 2012; Ladle et al., 2019). Therefore, including measures of variability in human activity over space and time increases one's ability to accurately identify animal responses to human disturbance (Ladle et al., 2019). Despite the potential impacts on wildlife and the need to identify mitigating management, the literature on disturbance caused by human activity on brown bears, especially in Europe, is relatively limited (Fortin et al., 2016).

This topic is of great relevance in the Italian Alps, an area characterized by a mosaic of natural and human-modified habitats, and a landscape fragmented by urban areas and roads where human presence is widespread, due to dense settlements and intense tourism presence (Oberosler et al., 2017; Tenan et al., 2017). Here, the local small bear population is the result of a reintroduction project in the central Italian Alps (Tosi et al., 2015), with the ultimate goal to recover functional ecological networks of meta-populations including the Dinaric-Pindos and Alpine (Kaczensky et al., 2012; Peters et al., 2015). Between 1999 and 2002, 10 brown bears from Slovenia were translocated to

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**Figure 1** – Map of the study area (left) in western Trentino province, central Italian Alps. The 60 camera trap locations are shown as black dots and the border of the Adamello-Brenta Natural Park (PNAB) is also shown. Brighter tones in the background correspond to higher elevation. The geographic location of the study area in Italy is shown in the map on the bottom-right. The study area is also shown inside the minimum convex polygon (MCP) occupied by brown bear females in western Trentino (courtesy of Large Carnivores Division, Forest and Wildlife Department, Autonomous Province of Trento [PAT]).

the Adamello-Brenta Natural Park (PNAB) in Trentino to re-establish a self-sustaining population. The last three remnant individuals were non-reproductive and died without any evidence of genetic exchange with the translocated bears and their progeny (Mustoni et al., 2003; De Barba et al., 2010a). From an ecological perspective, the project is to date an example of successful brown bear recovery in central Europe. After two decades, the population reached 82–93 bears, representing over the last 5 years an average growth rate of 12% (Groff et al., 2020). At the same time, however, as the population abundance increases, new conflicts with humans arise. This calls for a better understanding of the effects of different types of disturbance on bears, to identify which human-influenced factors are least compatible with brown bear conservation, and giving managers the knowledge to modulate the anthropogenic pressure (Swenson et al., 2000).

Here, we used camera trapping data collected consistently over 4 consecutive years coupled to activity pattern (Zimmermann et al., 2016) and occupancy (MacKenzie et al., 2002) analyses to investigate the effect of human activity on brown bear spatial and temporal patterns across the Alpine core area in western Trentino, Italy. In a single-year study in the same study area, Oberosler et al. (2017) found a crepuscular/nocturnal bear activity pattern likely induced by anthropogenic dis-

turbance, as documented by other studies across Europe (Kaczensky et al., 2006; Fortin et al., 2016), and a negative effect of human disturbance on bear detection probability. We used a more robust dataset and diverse pool of disturbance covariates than in Oberosler et al. (2017) to (i) reassess the temporal segregation pattern between bears and humans using the multi-year dataset, and (ii) explore the presence of spatial segregation within overlapping diel activity periods. By using images of people and vehicles at camera trap sites we could directly quantify the variability of human passage rates. Specifically, we aimed to address the following questions: (a) is there temporal segregation between bears and people? (b) In hours when both species are active, is brown bear occupancy influenced by anthropogenic sources of disturbance, both permanent (settlements) and/or variable (pedestrian/vehicle traffic)? (c) Does human disturbance also influence bear detection probability? We expected bear occupancy rates to be negatively related to the rate of human passage at sites, especially so by motorised traffic, and also hypothesized that bears avoid sites closer to human settlements. The alternative hypothesis we considered is that bear occupancy is not related to human activities, hence mainly driven by environmental factors.

**Table 1** – Covariates fitted in the occupancy model for the brown bear in crepuscular hours across the study area, central Italian Alps. The hypothesized relationships with detection ( $p$ ) and/or occurrence ( $\psi$ ) probabilities, respectively, are also indicated.

| Covariate                                    | Description   | Submodel      | Hypotheses  |
|--|---|---------------|---|
| Camera-trapping rate of pedestrians/bikes    | $\frac{N \text{ of independent events}}{\text{camera days}} 100$  | $\psi$<br>$p$ | Bears avoid sites of high human passage.<br>Behavioural response: bear increased shyness negatively affects detection probability.  |
| Camera-trapping rate of (motorised) vehicles | $\sqrt{\frac{N \text{ of independent events}}{\text{camera days}}} 100$   | $\psi$        | Passing vehicles negatively affect bear occurrence probability.   |
| Distance to settlements                      | Distance (m) of camera trapping sites to closest settlement. It is also a proxy for distance to major road network and elevation across the study area. | $\psi$        | Human settlements decrease bear's site use due to human disturbance. Bear occurrence probability negatively affected by human proximity both in North America and Europe.   |
| Terrain slope                                | Slope in degrees  | $\psi$        | Site use positively associated with inaccessible, rugged areas, especially during hours of activity overlap between bears and people.   |
| Type of track                                | Binary covariate (0-1) for the type of track monitored: forestry roads or hikers/hunters trails. Proxy for vehicle traffic.                             | $p$           | The type of track may influence detectability of species, according to the animal behaviour linked to the path selected to move. Expected higher occurrence probability on trails with much less motorised traffic. |

## Materials and Methods

We conducted our study in an area of about 220 km<sup>2</sup> in the central Italian Alps (centred on 46°6'45" N and 10°55'50" E; Fig. 1). This mountainous area encompassed the southern part of the Brenta group, the westernmost Dolomite group, and its adjacent valleys, which are partially included within the PNAB. The sampling area holds part of the core area of the brown bear population (Groff et al., 2020) and represents a large variation in both habitat type and altitudinal range (300–2800 m a.s.l.), with a dominant mountainous terrain. Tourists contribute largely to human activity in the summer across the study area. Camera trapping data were collected yearly during 2015–2018. Every summer season (June–September), Reconyx HC500 (Reconyx Inc., Holmen, WI, USA) and UOVision UV572 IR+ (UOVision Technology, Shenzhen, China) camera traps, the latter model used only at 50% of sites in the first year of sampling, were placed in the field for a total of 60 sampling sites (Fig. 1). Sites were initially positioned at random across the study area, one for each 4 km<sup>2</sup>-cell of a regular grid designed to uniformly sample an altitudinal gradient from 500 to 1900 m a.s.l. and so being representative of the habitat variation. Once in the field, being the area diffusely covered by forestry roads and trails, which we considered suitable sites for detecting both passing wildlife and humans, sampling sites were adjusted to fall equally on these categories. The sampling was done through two sequential arrays of 30 camera traps each, for easier implementation and due to limited equipment available. The sampling season included both the period when bears were active and when human presence, mainly due to tourism, was highest across the study area. Every sampling season, each camera was deployed for a minimum of 30 days (generally 30–35 days) and placed on a tree to record a trail segment approximately 2–4 m away. For other details about the study area and data collection see Oberosler et al. (2017).

By following the procedure described in Ridout and Linkie (2009), we investigated overall daily activity patterns of brown bears and people across the study area over the 4-year period. First, we subsampled the raw data for consecutive detections of brown bears and people at each site recorded within 30 min (Yasuda, 2004; Rovero and Spitale, 2016; Zimmermann et al., 2016). We estimated the coefficient of overlapping  $\Delta$  (ranging from 0, no overlap, to 1, complete overlap) using the package `overlap` in R (Meredith and Ridout, 2014), and also assessed the significance of the difference between daily patterns (Rovero and Zimmermann, 2016).

To assess spatial occurrence probability of bears in relation to human disturbance, we extracted from the total dataset all images obtained in time intervals 05:00–10:00 am and pm, respectively (hereafter referred to as “crepuscular” hours). These were arbitrarily defined, based on the results of the activity pattern analysis (this study and Oberosler et al., 2017), to include peaks in overlap of bear and human diel activity. Crepuscular detections of the brown bear during the entire sampling period were summarized in an array,  $Y$ , with elements  $y_{i,t}$ , which denoted the total number of detections for the brown bear at site  $i$ , during year  $t$ . We used a sampling duration of 5 days to define temporal replicates, which led to a median of 8 total sampling occasions  $K_{i,t}$  among different sites and years. We carried out single-species occupancy analysis using a hierarchical modelling framework (MacKenzie et al., 2002).

We specified the detection model for the observational data,  $y_{i,t}$  for the brown bear at site  $i$  in year  $t$  as  $y_{i,t} \sim \text{Bin}(p_{i,t} \cdot z_{i,t}, K_{i,t})$ , where  $p$  is the detection probability of bears at site  $i$  in year  $t$ , conditional on species presence ( $z = 1$ ), and  $K_{i,t}$  is the number of sampling occasions at site  $i$  in year  $t$ . We expected bear increased shyness and lower detection probability  $p_{i,t}$  with increasing intensity of pedestrian passage, defined as a detection rate (denoted  $PED$ , events discretized using 15 min as interval between consecutive events; see Tab. 1). We were also interested in whether there was an association between detectability and the type of track ( $TRAIL$ ). We hypothesized a negative effect of forestry roads as compared to trails, due to vehicular traffic. In addition, we also included a fixed year effect to the linear predictor for detectability to account for variability across years ( $YEAR\_P$ ), where year 1 is the

reference year:

$$\text{logit}(p_{i,t}) = \beta_0 + YEAR\_P_t + \beta_1 \cdot PED_{i,t} + \beta_2 \cdot TRAIL_i \quad (1)$$

Occurrence was modelled as a Bernoulli random variable,  $z_{i,t} \sim \text{Bern}(\psi_{i,t})$  with probability  $\psi_{i,t}$ , where  $z = 1$  when the species was present at site  $i$  during year  $t$ , and zero otherwise. We modelled occurrence probability as a function of both pedestrian and vehicle passage rates at sites, as detected by camera traps during each sampling season in crepuscular hours ( $PED$  and  $VEH$ , respectively). We also included distance from settlements ( $VILLAGE$ ) and terrain slope ( $SLOPE$ ) in the linear predictor for occupancy (Tab. 1). Finally, we added a fixed year effect to account for variability across years ( $YEAR\_PSI$ ). We defined the logit transformation of the occurrence probability as follows:

$$\text{logit}(\psi_{i,t}) = \alpha_0 + YEAR\_PSI_t + \alpha_1 \cdot PED_{i,t} + \alpha_2 \cdot VEH_{i,t} + \alpha_3 \cdot VILLAGE_i + \alpha_4 \cdot SLOPE_i \quad (2)$$

We considered this model formulation because we wanted to investigate the global effect of disturbance on bear’s occupancy, rather than on colonization and extinction components. However, we acknowledge that, contrary to an auto-logistic parameterization, the one we used does not account for correlated binary (i.e. occupancy) processes. We considered fixed-time effects for year because the number of years was too low to ensure reliable estimates of temporal random variance. Moreover, since estimating site-specific variance requires at least 6 detections per site (Gelman, 2006), and in our case only 5% of sites reached that amount of detections across the whole study period, we did not account for variation in occupancy at the site level unexplained by the covariates. Finally, we are aware of the potential issues related to the interpretation of occupancy estimates in camera trapping studies (Efford and Dawson, 2012; Neilson et al., 2018). However, we considered occupancy as the proportion of the sampled area used by the species during the focal diel period, i.e., occupancy rate, and based our inference on this metric, with our main focus being the covariate effects on occupancy rates.

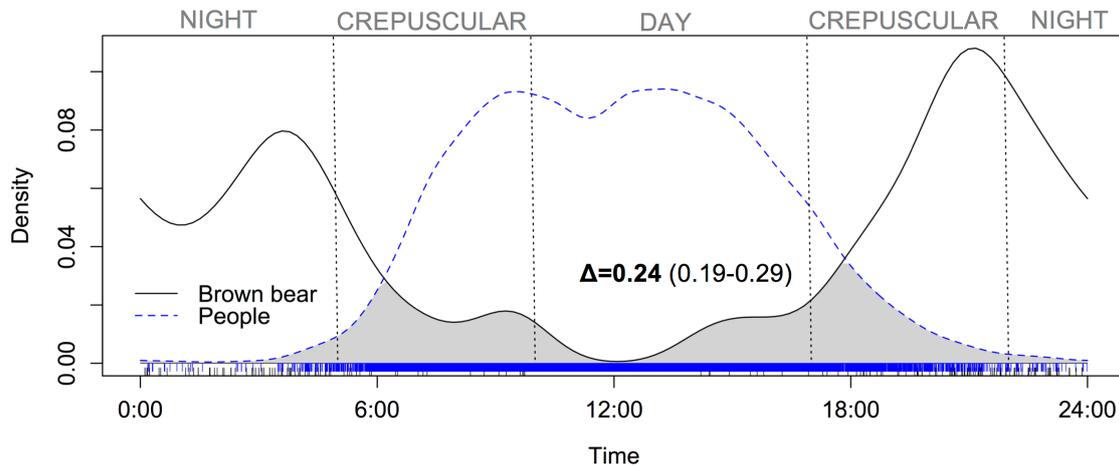
We assessed the degree of support for each covariate in the linear predictors for detection and occupancy probability by calculating the posterior variable inclusion probability ( $Pr(\omega = 1)$ ), i.e. the probability that a variable is “in” the model, using the Gibbs Variable Selection (GVS) approach (O’Hara and Sillanpää, 2009; Tenan et al., 2014). For each parameter  $\theta = \{p, \psi\}$ , the GVS process involves each coefficient ( $\beta_1$ – $2$  and  $\alpha_1$ – $4$ ) being multiplied by a binary “inclusion parameter” ( $\omega_{\theta, cov} = 1$  if present in the model, and 0 if not), with a Bernoulli prior distribution with parameter 0.5. The corresponding “full” linear predictors were as follows:

$$\begin{aligned} \text{logit}(p_{i,t}) &= \beta_0 + YEAR\_P_t + \omega_{p, PED} \cdot \beta_1 \cdot PED_{i,t} + \\ &\quad \omega_{p, TRAIL} \cdot \beta_2 \cdot TRAIL_i \\ \text{logit}(\psi_{i,t}) &= \alpha_0 + YEAR\_PSI_t + \omega_{\psi, PED} \cdot \alpha_1 \cdot PED_{i,t} + \\ &\quad \omega_{\psi, VEH} \cdot \alpha_2 \cdot VEH_{i,t} + \omega_{\psi, VILLAGE} \cdot \alpha_3 \cdot VILLAGE_i + \\ &\quad \omega_{\psi, SLOPE} \cdot \alpha_4 \cdot SLOPE_i \end{aligned} \quad (3)$$

The posterior mean of  $\omega_{\theta, cov}$  therefore represents the posterior inclusion probability for the covariate in the model. Model-averaged parameter estimates were derived. A “slab and spike” prior for coefficients  $\beta_1$ – $2$  and  $\alpha_1$ – $4$  was used to improve the mixing and convergence time of the MCMC algorithm (O’Hara and Sillanpää, 2009). Prior probability for each coefficient,  $\beta_1$ – $2$  and  $\alpha_1$ – $4$ , was specified as a mixture of normal distributions:

$$Pr(\beta_1 | \omega_{p, PED}) = (1 - \omega_{p, PED}) \text{Norm}(0, 1) + \omega_{p, PED} \text{Norm}(0, \Sigma) \quad (4)$$

taking  $\beta_1$  as an example, where the fixed prior variance  $\Sigma = V/(l+1)$ , with  $l$  denoting the number of regressors in the linear predictor and the total variance in the linear predictor  $V$  with a  $\text{Gamma}(3.2890, 7.8014)$  prior assigned (Link and Barker, 2006).



**Figure 2** – Diel activity patterns (kernel density curve) for the brown bear over the 4-year period in the study area, central Italian Alps, and its overlap with human activity (dashed line). The dotted vertical lines delimit the crepuscular window of time considered in the occupancy analysis. The coefficient of overlap ( $\Delta$ ) and relative confidence interval are also reported.

We fit the model using a Bayesian formulation and Markov chain Monte Carlo using JAGS (Plummer, 2003), called from R (R Development Core Team, 2016) through the package `jagsUI` (Kellner, 2016). We ran 3 chains of length 250000, discarded the first 10000 iterations as burn-in, and thinned the remaining results by taking each 20<sup>th</sup> value from the chains, yielding 36000 total samples from the joint posterior. Covariates were standardized to have mean zero and unit variance. We assessed convergence through visual inspection of the chains and with the Gelman-Rubin diagnostic (Brooks and Gelman, 1998). For further details about the model we refer to the supplementary code (Data S1).

## Results

Sampling over the 4-year period yielded 181 and 11466 independent events (considering a time threshold of 30 minutes) of bears and people, respectively, which were included in the activity pattern analysis. Results showed a predominantly crepuscular and nocturnal behaviour for the brown bear across the study area over the 4-year sampling seasons. Activity peaked before dawn (04:00 am) and after dusk (09:00 pm). Brown bear activity curve was significantly different from that of humans, with a coefficient of overlap of  $\Delta=0.24$  (0.19–0.29,  $p<0.00001$ ) (Fig. 2).

Results of variable selection for spatial analysis in crepuscular hours, which considered a total of 78 detections of brown bear, indicated that the most supported predictor of brown bear occupancy was distance to settlements ( $\omega_{\psi,VILLAGE}=0.99$ ), with a positive and significant effect ( $\alpha_3$ : model-averaged posterior mean 0.92, 95% Bayesian credible interval [BCI] 0.38–1.56; Tab. 2 and 3, Fig. 3). The vehicular traffic rate also had a significant, negative effect on bear occupancy ( $\alpha_2$ : mean  $-0.84$ , 95% BCI  $-1.74$ – $-0.06$ ), with an inclusion probability  $\omega_{\psi,VEH}=0.76$ . Similarly, the pedestrian passage rate had a negative effect, but the 95% BCI overlapped zero ( $\alpha_1$ : mean  $-0.51$ , 95% BCI  $-1.28$ – $0.33$ ) and the inclusion probability was  $<0.5$ . Despite that, the

**Table 2** – Inclusion probabilities ( $\omega_{\theta,cov}$ ) for the covariate effects on detection and occurrence probability, respectively, for the occupancy model of the brown bear in western Trentino, central Italian Alps. Values are based on Bayesian model selection using Gibbs variable selection. PED: pedestrian passage rate; TRAIL: type of track; VEH: vehicle passage rate; VILLAGE: distance from settlements; SLOPE: terrain slope.

| Parameter | Covariate | $\omega_{\theta,cov}$ | Probability of significant effect |
|-----------|-----------|-----------------------|-----------------------------------|
| Detection | PED       | 0.369                 | 0.91                              |
|           | TRAIL     | 0.422                 | 0.91                              |
| Occupancy | PED       | 0.488                 | 0.91                              |
|           | VEH       | 0.764                 | 0.99                              |
|           | VILLAGE   | 0.989                 | 1.00                              |
|           | SLOPE     | 0.178                 | 0.51                              |

probability of a negative effect for this covariate was high (0.91; Tab. 2 and 3, Fig. 3). Terrain slope showed no effect ( $\alpha_4$ : mean  $-0.01$ , 95% BCI  $-0.50$ – $0.47$ ) and low probability of significant effect (0.51). As for bear detection probability, the type of track showed high probability of significant effect (0.91), with a positive effect of trails as compared to forestry roads, even if the 95% BCI overlapped zero ( $\beta_2$ : mean 0.46, 95% BCI  $-0.20$ – $1.15$ ). Finally, the pedestrian passage rate also showed a negative effect on bear detection probability ( $\beta_1$ : mean  $-0.34$ , 95% BCI  $-0.85$ – $0.18$ ; Tab. 2 and 3, Fig. 3). There was no significant variability across years in estimated detection and occurrence probabilities (see Tab. S2).

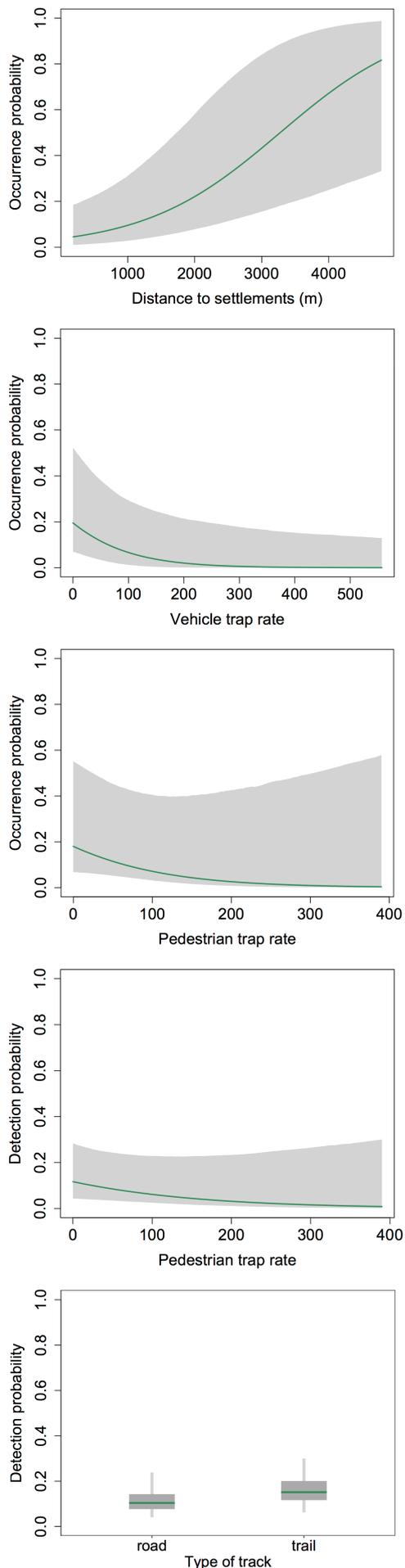
## Discussion

Our results suggest that human activity and settlements affect brown bears in the central Italian Alps through both temporal and spatial displacement. The analysis of activity patterns brought evidence of the temporal niche segregation between bears and people, with bears being active mostly during the night and in crepuscular hours, and human activity typically being high during daylight. As for the spatial analysis, motorised traffic seemed to negatively influence both occurrence and detection probability; moreover, detection probability was higher on trails than forestry roads. Similarly, we found a marked and positive association between distance to settlements and brown bear occupancy. Additionally, the rate of pedestrian passage showed a marginally significant and negative effect on both model components.

These results are partially consistent with preliminary findings from the same study area on the baseline year of data collection (Oberosler et al., 2017). The coefficient of overlap between daily activity of bears and peoples for the 4-year period is particularly consistent with that on 2015 data for sites with lower human disturbance. This is likely because the majority of bear detections in the multi-year dataset were from sites where human activity was relatively lower. Brown bear's switching from diurnal to crepuscular or nocturnal activity likely to avoid encounters with people has already been documented for other bear populations across Europe (Olson et al., 1998; Kaczensky et al.,

**Table 3** – Model-averaged posterior estimates for the effects of covariates on occurrence and detection probabilities, respectively.

| Parameter                            | Mean (SD)      | q2.5    | q50     | q97.5   |
|--------------------------------------|----------------|---------|---------|---------|
| $\alpha_1$ , pedestrian passage rate | $-0.51$ (0.40) | $-1.28$ | $-0.51$ | 0.33    |
| $\alpha_2$ , vehicle passage rate    | $-0.84$ (0.42) | $-1.74$ | $-0.82$ | $-0.06$ |
| $\alpha_3$ , distance to settlements | 0.92 (0.30)    | 0.38    | 0.90    | 1.56    |
| $\alpha_4$ , terrain slope           | $-0.01$ (0.25) | $-0.50$ | $-0.01$ | 0.47    |
| $\beta_1$ , pedestrian passage rate  | $-0.34$ (0.26) | $-0.85$ | $-0.34$ | 0.18    |
| $\beta_2$ , type of track            | 0.46 (0.34)    | $-0.20$ | 0.45    | 1.15    |



**Figure 3** – Significant effects of covariates on occurrence and detection probabilities of the brown bear across the study area (Trentino, central Italian Alps), as assessed within crepuscular hours (05:00–10:00 am and pm). Lines show the posterior mean, while grey polygons show the 95% BCIs.

2006; Fortin et al., 2016). Indeed, this predominantly “shy” behaviour is typical of carnivores, which show diurnal activity in remote areas and often become more nocturnal when in human-dominated landscapes (Ordiz et al., 2017). In North America, for example, where areas inhabited by bears are generally characterized by low intensity of human utilization, brown bears seem largely diurnal (Klinka and Reimchen, 2002) and more aggressive than their European counterparts (Swenson et al., 1999).

Our results of bear spatial analysis are consistent with previous studies across Europe that identified spatial displacement as one of the most common impacts of human recreational activities on bears, specifically with bears avoiding areas close to humans and leaving areas in response to humans (Fortin et al., 2016). Patterns of spatial avoidance of roads and trails with high human passage, especially motorised traffic, have also been documented for grizzly bears (Northrup et al., 2012; Ladle et al., 2019). Specifically, our results identified distance to settlements as one of the strongest predictors of bear occurrence probability. In this regard, we note that distance to settlements is partially collinear ( $r=0.6$ ) with elevation, hence the significance of this former covariate may reflect habitat preference rather than disturbance avoidance. At the same time, however, the negative effect of human passage (both vehicles and pedestrians) was significant and independent of elevation ( $r=0.2$  and  $0.3$  for motorised and non-motorised traffic, respectively). Hence, that both distance to settlements and human passage are positively associated with occupancy estimates suggests that the detected effects were likely a response to disturbance. Terrain slope was included to test an alternative hypothesis that may explain variability in brown bear occupancy, with bear potentially showing preference for steep and inaccessible locations. However, it seemed to have no effect on bear spatial activity in crepuscular hours across the study area. This is potentially explained by the fact that we sampled part of the brown bear core area, below the tree line, and suggests that direct sources of human disturbance are stronger drivers of bear occupancy. Bear detection probability was negatively related to the intensity of pedestrian passage and roads accessible to vehicular traffic, as compared to trails. Such results, consistently with the ones for occupancy, suggest a pattern of increased elusiveness caused by both pedestrian and vehicles. Indeed, such effects are compatible, given that camera traps detected a very high pedestrian passage also on forestry roads open to traffic, especially in proximity of ski lift or close to lodges/restaurants. We note that our spatial analysis did not take into account the whole 24-h period as we explicitly aimed to detect potential patterns of human avoidance by bears in hours when activity patterns overlapped. Hence during the remaining diel period, particularly at night when most of the residual detections of bears occurred, the patterns we found may be less pronounced. Indeed, that Oberosler et al. (2017) did not find an effect of distance to disturbance on occupancy suggests that the presence of people during activity overlap is a more important driver of site use than the mere distance to permanent sources of disturbance.

Our study offers new insights into spatio-temporal patterns of the only Alpine bear population, and provides for a case study where we could quantify bear and human activity simultaneously and at the same spatial scale. Furthermore, the extensive sampling with camera traps, consistent over the 4-year period, allowed us to investigate both spatial and temporal patterns of human avoidance by bears using the same dataset. The area inhabited by the study population has one of the highest human population densities among those occupied by brown bears (De Barba et al., 2010b; Chapron et al., 2014). Ski lifts, which are operational also during the summer to facilitate mass influx of tourists, largely contribute to generate high levels of anthropogenic passage. Interestingly, by sampling and monitoring an area that is partially inside the PNAB, we could detect a lack of substantial differences in disturbance rates, motorised traffic and infrastructure development between inside and outside the protected area.

The small brown bear population of the central Italian Alps is of remarkable importance for conservation: it is subject to high rates of anthropogenic mortality (Tenan et al., 2016), has no immigration, and its density steadily decreases from the point where founders were re-

leased, indicating their limited dispersal ability (Tenan et al., 2017). Indeed, its core range in Trentino is a key requisite for the purpose of facilitating the establishment of the larger Alpine population in the future (Mustoni et al., 2003; Linnell et al., 2008; Groff et al., 2015; Peters et al., 2015). Yet, connectivity of this population remains a concern at multiple spatial scales (Peters et al., 2015). The Habitat Directive provides full protection for brown bears in the European Union under Annex II and IV (Kaczensky et al., 2012). In this context, evaluations of the impact of human activities and infrastructures on bear habitat and behaviour are required actions at both international and national levels (Swenson et al., 2000).

The negative effect of public motorised traffic we revealed should be taken into consideration by managers as one of the human-influenced factors that are least compatible with brown bear activity. With the awareness that overregulation would be detrimental to public acceptance of bears (Swenson et al., 2000), the construction of forestry roads for public use and other roads for resource extraction should be restricted/regulated, especially in critically important areas (such as the PNAB territory). Although caution in interpretation is needed given the small sample size, our results deliver a reassuring message for forest users and managers and provide more evidence that bears living in human-modified landscapes have developed a solid pattern of human avoidance. This is an important prerequisite for the coexistence of brown bears and people in the study area and the Alps in general, and is especially relevant in the current context of increasing human-bear conflicts. 🐾

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## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

**Data S1** R and JAGS code for the single-species occupancy model, model selection and averaging.

**Table S2** A. Summary of posterior parameter estimates from the brown bear occupancy model; B. Na ve occupancy for the brown bear in the 4-year study period across the study area.