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Human-induced risk drives behavioural decisions in a recovering brown bear population

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Abstract

In human-dominated landscapes, rebounding bear populations share space with people, which may lead to bear–human conflicts and, consequently, a decrease in acceptance and an increase in bear mortality linked to human causes. Previous analyses of brown bear (*Ursus arctos*) movement data have shown that bears adopt a security-food trade-off strategy in response to variable human-related risk. However, brown bear flexibility to cope with these risky situations may be reduced when resting, mating or stocking fat in preparation for hibernation. In this study, we measured the multi-scale spatial response of brown bears to human-related risk and food resource distribution in a highly heterogeneous human-dominated landscape. We examined habitat selection both within the population range ('second-order' selection) and at bedding site locations ('third-order') for GPS-tagged brown bears of a recently reintroduced population in the Italian Alps. We identified resting locations by field-validated spatio-temporal cluster analysis of telemetry locations. We mapped food availability and distribution using dynamic geographic layers of fruiting wild berries, and human-related risk using human mobility data (Strava-based Cumulated Outdoor activity Index). Brown bears appeared to compromise their need for food resources for avoidance of anthropogenic disturbance when selecting home ranges, as they utilized areas richer in wild berries less when human use of outdoor tracks was higher. Furthermore, selection of resting site locations strongly depended on the avoidance of human-related risk only, with less frequented, more concealed and inaccessible sites being selected. We conclude that humans compete for space with bears beyond their infrastructural impact, that is, by actively occupying key areas for bear survival, thereby potentially restricting the bears' realized niche. We propose mitigating actions to promote bear–human coexistence by selectively restricting human access to key areas during sensitive annual physiological phases for bear survival.

Introduction

As land use by humans increases dramatically around the world (Foley *et al*., 2005) and recreational activities spread beyond urban contexts (Knight & Gutzwiller, 1995), the spatial overlap between humans and wildlife is intensifying. In the landscape, humans–wildlife competition for space emerges as structural (e.g. roads) and functional (e.g. actual presence of humans) disturbances (Ellis-Soto *et al*., 2023). This exposes a growing number of species to direct risk (i.e. human-caused mortality; Creel & Christianson, 2008), inducing behavioural responses (Tuomainen & Candolin, 2011). Animals may respond by displacing into safer and less disturbed habitats (Martin *et al*., 2010), by adjusting their activity cycles (Gaynor *et al*., 2018) or both (Schuette *et al*., 2013). For example, fear of humans can change diel activity patterns (Bonnot *et al*., 2020) or habitat use (Salvatori *et al*., 2022) in large herbivores; or reduce feeding time in medium-sized (Suraci *et al*., 2019) and large carnivores (Smith *et al*., 2017). Understanding how species respond to different types of anthropogenic disturbance is becoming central in ecology and conservation (Rutz *et al*., 2020). The relative effect of anthropogenic disturbance varies by observation scale (Levin, 1992); hence, some responses to human disturbance only emerge at specific scales of inference (Ciarniello *et al*., 2007; Suraci *et al*., 2019; Nisi *et al*., 2022).

Coexisting with humans is costly: in addition to human-induced mortality, such as vehicle collision, poaching or culling, animals sustain additional physiological or energetic costs as a result of adopting antipredator behavioural responses to human presence, such as the aforementioned changes in habitat use, vigilance or feeding habits (i.e. risk effect; Creel & Christianson, 2008). Large carnivores are no exception, with humans ‘super predators’ regarded as an integral part of their ecosystem, echoing a predator–prey relationship (Chapron & López-Bao, 2016; Smith *et al*., 2017). Risk perception by large carnivores may vary with spatial and resource requirements across different ‘biologically sensitive’ periods (i.e. resting, mating, or fattening up for hibernation; *sensu* Yovovich *et al*., 2020). For some species, food intake is particularly critical at certain times of the year (e.g. hyperphagia before entering hibernation; Swenson *et al*., 2020; or weaning in grey wolf *Canis lupus*; Sand *et al*., 2008). A human-induced landscape of fear can compromise access to these resources (Lodberg-Holm *et al*., 2019), with cascading consequences on individual fitness if disturbance is high. Furthermore, at the diel scale, resting is an especially vulnerable behavioural phase as animals have a much lower ability to cope with risky situations due to minimal mobility (Lima *et al*., 2005). Understanding how species respond to human disturbance during annual physiological phases at multiple spatial scales is therefore pivotal for the long-term conservation of carnivores.

Brown bears (*Ursus arctos*) are among the world’s largest carnivores, yet they show fear reactions to encounters with humans (Moen *et al*., 2012; Støen *et al*., 2015), suggesting that individuals perceived human-derived risk and adopted behavioural strategies to reduce risk exposure (i.e. antipredator response; Ordiz *et al*., 2013). Further, unlike most other large carnivores, they need to store enough energy during their active months to sustain 3 to 7 months of hibernation and pregnancy. This is important for their life cycle and, consequently, for their survival and reproductive capacity, particularly in females (Robbins *et al*., 2012). Nevertheless, bears’ ecological plasticity and especially their omnivory allows them, on the one side, to modify their diet based on physiological needs and variations in food resource availability (Mowat & Heard, 2006); on the other side, to live in a broad range of environments, some of which are characterized by significant levels of human encroachment (McLellan *et al*., 2017). In Europe, for example, despite a remarkable recovery of large carnivores over the past decades (Chapron *et al*., 2014), the availability of suitable habitats for brown bears is still largely determined by human population density (Cimatti *et al*., 2021). Hunting has also been demonstrated to have a considerable impact on their life history (Bischof *et al*., 2018), while some populations remain geographically isolated and exhibit low genetic variability due to past human persecution and current lack of habitat connectivity (Kaczensky *et al*., 2012).

The expanding population of brown bears living in the Central Alps represents one of the most emblematic examples of recovery in human-dominated Europe. Reinforced through a reintroduction project in the early 2000s (Duprè, Genovesi, & Pedrotti, 2000), the population has settled in Western Trentino, an area with relatively high human encroachment, and is currently estimated to be around 100 individuals (Groff *et al*., 2022). However, despite significant improvement, the population is currently listed as Critically Endangered due to the small number of mature individuals (<50, Criteria D1; IUCN, 2001) (Huber, 2018). Adult survival is still mainly driven by anthropogenic mortality (Tenan *et al*., 2016), with a significant proportion of road-kills and poaching (Groff *et al*., 2022). In this context, alpine brown bears have been shown to respond to the functional presence of humans, with human mobility significantly reducing habitat connectivity (Corradini *et al*., 2021b), while human outdoor recreation activities limit the use of suitable space (Corradini *et al*., 2021a). Such evidence shows that bears in the Alps are currently exposed to multiple sources of anthropogenic disturbance (Morales-González *et al*., 2020), with humans acting as direct competitors for space, hence potentially constraining the bears’ realized niche (*sensu* Hutchinson, 1957) and leading to conflicts (PACOBACE, 2010). Yet, a multi-scale spatial evaluation of human-derived risk responses of this reintroduced population and derived indications for conflict mitigation are lacking.

In this study, we aimed to assess the effect of multi-scale anthropogenic disturbance on behavioural decisions by bears. Specifically, we intended to characterize the behavioural trade-off between risk avoidance and seasonal resource selection at two ecologically relevant scales: the home range selection within the population range and resting site location. Using the Alpine bear population, and newly developed covariates for this region, we tested two main hypotheses: (i) when selecting for home ranges within their population range (‘second-order’ of selection; Johnson, 1980), bears should weigh their energetic requirements in different annual physiological phases against risk perception, while accounting for seasonal resource availability. We modelled bears’ resource selection in dependence of topographic variability, habitat productivity, functional anthropogenic disturbance (i.e. Cumulated Outdoor activity Index, a Strava-derived index of disturbance; Corradini *et al*., 2021a) and monthly resource availability (i.e. seasonal fruit richness index; Tattoni *et al*., 2019), interpreted against their main annual physiological phases (hypophagia, mating season and hyperphagia); (ii) when selecting for resting sites within their home range (‘third-order’; Johnson, 1980), bears should prioritize areas with low functional anthropogenic disturbance, even to the detriment of resource proximity, by applying a security-food trade-off strategy (Cristescu, Stenhouse, & Boyce, 2013). For this purpose, we modelled the individual selection of resting sites in dependence of topographic variability, human-derived risk perception, forest canopy structure and monthly resource availability.

Materials and methods

Study area and brown bear movement data

The research was conducted in the province of Trento, commonly known as Trentino (10.5°E, 45.6°N – 12.0°E, 46.5°N), a mountainous region in the Central-Eastern Italian Alps (Fig. 1). The area covers 6200 km^2 within the Alpine biogeographical region (EEA, 2002) and is characterized by a complex set of microclimates due to a morphologically diverse landscape (from 65 to 3.769 m a.s.l.). The slopes are characterized by dense forest cover, followed by alpine grasslands in the upper portions and bare terrain at the highest altitudes. The valleys have the highest concentration of human presence: they are densely populated (187 people km^{-2} below 600 m a.s.l.) and have a developed infrastructure network (95 km/100 km^2). The Adige valley, the region's largest and most developed valley (crossed by the homonymous river, a highway, a railway, as well as numerous minor roads and urban areas; Fig. 1), poses a major threat to ecological connectivity for many animal species, including the brown bear (Peters *et al.*, 2015).

Between 2006 and 2019, 18 adult bears (11 females and 7 males) were captured throughout the study area and fit with GPS collars (Vectronic Aerospace GmbH, Berlin, Germany) as part of the management programme carried out by the Autonomous Province of Trento for bears target of monitoring (i.e. dwelling in proximity of human properties, exhibiting confident behaviour or having shown aggressive defensive behaviour: PACOBACE, 2010; Data S1 for details about bear trapping protocol). Bears were tracked for

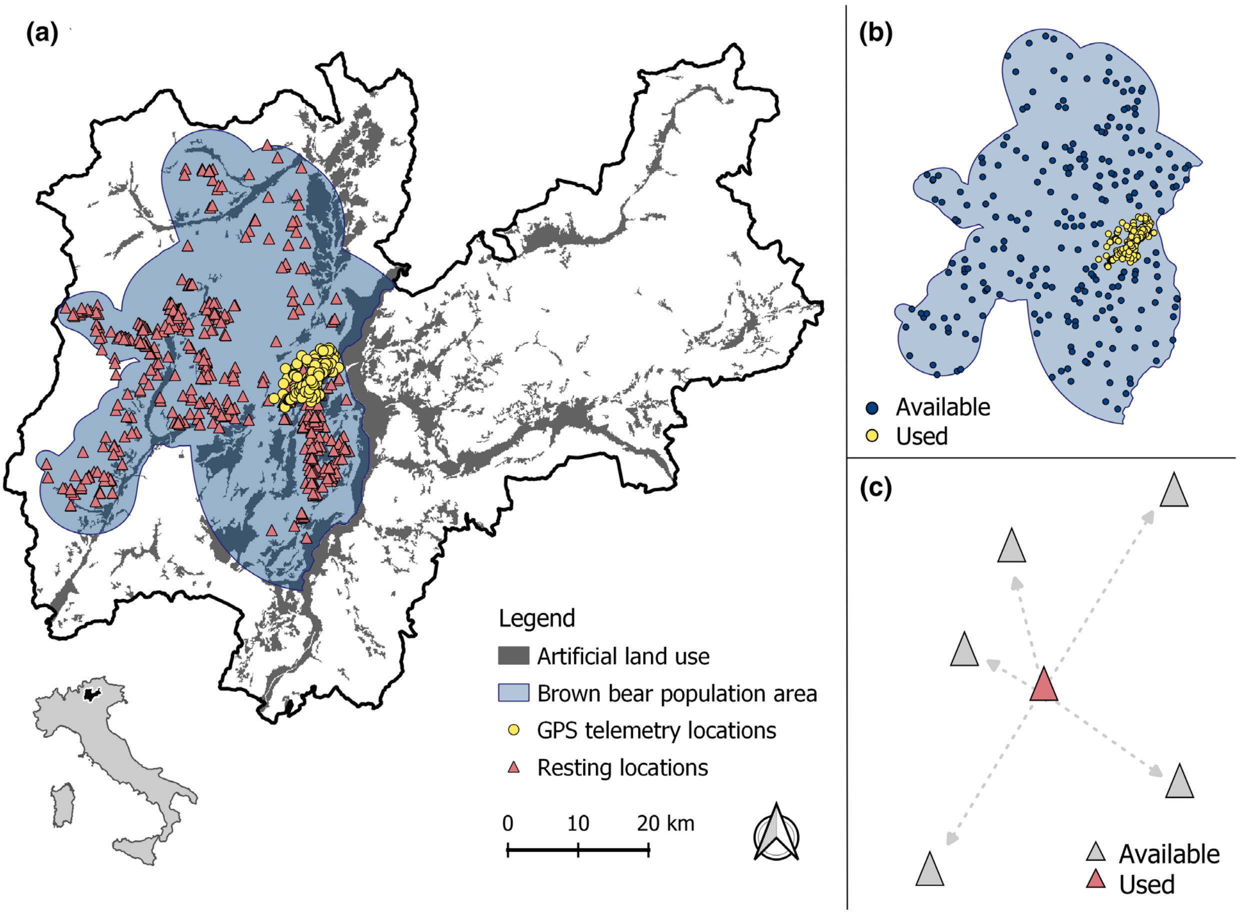

Figure 1 (a) Map of the study area and its location in the Italian Alps. The blue area indicates the brown bear population area, the yellow dots the GPS telemetry locations (for clarity, only the locations of one individual are shown), and the dark pink triangle the resting locations of all adult bears identified through spatiotemporal clustering. In light grey, the distribution of artificial surfaces (i.e. altered by humans). (b) Second-order selection: 'Available' points (shown in blue) selected at random from the population range, and yearly individual GPS locations ('Used', shown in yellow). (c) Resting site selection: 'Available' locations (shown in light grey) generated from the 'used' resting location (shown in dark pink) by resampling turning angles and step lengths from the empirical distribution.

management needs from one to several years, for a total of 44 animal-year (i.e. yearly location data for tracked individuals). GPS collar acquisition intervals varied between individuals, therefore we used different resolutions based on the type of ecological question we wanted to answer (second- vs. third-order). Following the methodology described by Urbano, Basille, & Cagnacci (2014), the GPS locations associated with impossible movement parameters (i.e. 'spikes') and locations (e.g. over a lake) as well as missing timestamp information were removed, leaving only 'valid locations' for analysis. Lastly, we subsetted the trajectories by only considering the GPS locations within Western Trentino (i.e. excluding dispersers; Fig. 1) and non-hibernating period (i.e. 1 April to 31 October), for a total of 6309 and 18 319 GPS locations for the second- and third-order, respectively.

Spatial covariates

It is particularly challenging to derive ecologically-meaningful covariates of anthropogenic disturbance and resource availability using field surveys and observations, especially in Alpine habitats, where field accessibility is a limiting factor. To overcome this constraint, and to later render region-wide spatial predictions, we used a set of newly developed covariates. These ecologically-meaningful covariates were obtained at the highest resolution available from a combination of space-, air- and human-borne sensors (Data S2 for a detailed description), specifically: we derived (a) Slope (*Slp*) from an airborne laser scanning survey (i.e. LiDAR, with an original spatial resolution of 2 m), a covariate known to be informative when modelling bear space use in the Alps (Peters *et al.*, 2015; Corradini *et al.*, 2021a); (b) Canopy Height Model (*CHM*) from the same data source (i.e. LiDAR) and (c) Tree Cover Density (*TCD*) using satellite imagery from the Copernicus Programme (Langanke *et al.*, 2017) as measurements of forest canopy vertical and horizontal structure, respectively. These covariates were used as proxies for perceived security towards human-derived risk (i.e. sites with lower canopy height and higher tree cover density should be perceived as more secure; Sahlén, Støen, & Swenson, 2011); (d) monthly Enhanced Vegetation Index (EVI) using multispectral satellite imagery from the NASA-MODIS sensors (with an original spatial resolution of 250 m) as a proxy for habitat quality and productivity (Pettorelli *et al.*, 2005; Zedrosser *et al.*, 2011); (e) the monthly fruit richness availability (*r-berry*) over the landscape of 44 plant species commonly eaten, or considered edible, by brown bears (Table S2.2) based on the GIS approach previously developed by Tattoni *et al.* (2019). The fruit richness maps were derived from vector maps of forest types (scale 1:10 000) and were used as a proxy for resource availability of high-quality food for bears. This was based on the analysis of their dietary habits, which showed a predominantly plant-based diet (De Barba *et al.*, 2014), and on the knowledge that fleshy fruits are an important part of the species' diet (García-Rodríguez *et al.*, 2021). Due to the lack of variability in species richness of fruiting plants, we discarded April and considered the richness of fruiting plants from May to October only. We included wild fruits in the analysis as they were widespread and readily available throughout the landscape, while alternative food sources were ephemeral and difficult to quantify, as their production (e.g. hard mast) and accessibility (e.g. orchards) were hardly measurable over large areas (e.g. region-wide); (f) the density of Cumulated Outdoor activity Index (*dCOI*) from a newly developed Strava-based index of human mobility (Corradini *et al.*, 2021a). The index was used as a proxy for functional anthropogenic disturbance, as it depicted a spatial variation of risk perception (Gaynor *et al.*, 2019). All covariates were resampled to a spatial resolution of 20 m pixel size, except for the EVI (with a resolution of 250 m), and were normalized by subtracting the mean and dividing by its standard deviation. We managed, processed and analysed spatial data through Free and Open-Source Software (FOSS), that is R 4.0.0 (R Core Team, 2020), QGIS 3.4.4 (QGIS Development Team, 2019) and GRASS 7.4 (GRASS Development Team, 2018) under Ubuntu 16.04.3 LTS (Canonical Ltd., London, UK).

Home range selection (second-order)

We modelled monthly resource selection at the population range via Resource Selection Functions (RSFs), with a use–availability design (Manly *et al.*, 2002). For each animal-year, GPS locations from bears monitored with a 6-h sampling protocol were considered as 'used' locations. The available space was defined by the population range, as indicated by the combination of all the annual individual 90% utilization distributions (Worton, 1989) calculated using the kernelUD function (with smoothing parameter = 'href') and extracted the area using the getverticeshr function in the R package 'adehabitatHR' (Calenge, 2006) and using the GPS locations of all individuals throughout the active season with availability of high-quality food for bears (i.e. May to October). We sampled for each animal-year 100 times as many resource units (i.e. 'available' locations) as the used GPS-based locations within such range to ensure stability in parameter estimates (Fieberg *et al.*, 2021). We spatio-temporally matched both used and available locations with the underlying covariates. We, therefore, estimated resource selection by fitting generalized linear mixed models (GLMMs) with a binomial error distribution via maximum likelihood, using a Laplace approximation, using the glmer function in the R package 'lme4' (Bates *et al.*, 2015). We assigned a weight W = 1,000 for each available sample, while keeping W = 1 for the used locations (Muff, Signer, & Fieberg, 2020). We fitted monthly models including ecologically-meaningful, non-collinear covariates as fixed effects (Pearson correlation coefficient $|r| \leq 0.6$; Figure S2.3). For each month (from May to October), we fitted a model including slope (as both linear and quadratic effect to account for potential nonlinear relationships, as we expect a negative relationship at very high levels of slope) and density of COI (dCOI) as static variables, while the EVI and species richness of fruiting plants (r-berry) as dynamic (i.e. monthly-varying) variables. Because TCD and CHM were positively correlated with one another and with EVI, we did not include them in the models. We considered an interaction term between the species richness of fruiting plants and the density of COI to better understand the link between the selection of high-quality resources and avoidance of human-derived risk, that we evaluated against the additive-only model by AIC, and, for equally likely models, Chi-squared based difference in deviance. We included individuals as random intercepts to account for among-individual variability (Gillies *et al*., 2006). However, for this study, we estimated marginal (population-level) responses only. We fitted a model for each month because fruit richness varies considerably throughout the year (Data S2), thus avoiding biased model output due to varying availability (Boyce & McDonald, 1999). For further interpretation of these models, we considered the following annual physiological phases of brown bears: (i) hypophagia and mating season: from 1 May to 31 July; (ii) hyperphagia: from 1 August to 30 October.

Resting site selection (third-order)

Resting sites were identified using a spatiotemporal clustering method, thereby GPS locations were grouped based on their spatial and temporal proximity. We used a higher protocol sampling for this analysis by selecting individuals whose GPS collar acquisition interval was at least 3 hours and filling any gaps in the sampling via linear interpolation. In practice, we identified hotspots (clusters) of use (i.e. potential resting sites) using the R package 'recurse' (Bracis, Bildstein, & Mueller, 2018), based on *ad hoc* parameterization. First, a circle with a radius of 25 m was drawn for each GPS location, and the time spent inside that buffer was determined using each GPS location's timestamp within that radius. Next, we categorized every cluster as a 'resting site' when it included locations for at least 9 consecutive hours (Figure S3), that is, at least four fixes. We chose a detection radius of 25 m to account for GPS measurement error and a time interval larger than 9 h to reduce the detection of non-target hotspots (i.e. foraging areas) while having a consistent detection even in case of missing values (e.g. for sites under dense canopy cover). We used the highest resolution available, even though in related studies, resting locations were identified using even higher sampling rates (Cristescu, Stenhouse, & Boyce, 2013; Skuban, Find'o, & Kajba, 2018). This was done to trade off the inclusion of as many individuals as possible (for meaningful population-level inference), with robustly identified resting sites. When multiple buffers that were designated as 'resting sites' overlapped, the centroid based on all neighbouring clusters was generated and that location was considered for the analysis. We also discarded any revisit of the same resting site to reduce autocorrelation problems. Last, we performed field validation to assess the cluster analysis' capacity to identify actual resting sites (false positive rate; Data S3 for specifications on field validation).

We considered the selection of resting sites within their home range as a discrete choice influenced by movement; therefore, we opted for a matched case–control approach where each resting site location is matched with a conditional set of available locations, which represented a stratum. We applied a mixed Conditional Logistic Regression (CLR) to model individual resource selection, using the mixed-effects cox model from the R packages 'coxme' (Therneau, 2020). Each resting site (i.e. the case) was paired with 25 random points (i.e. the controls) generated from the resting site centroid by resampling turning angles and step lengths from the empirical distribution (Fortin *et al*., 2005) of brown bear 3-h GPS locations. We assessed the individual selection of resting sites with respect to topography, forest structure, resource availability and anthropogenic disturbance by spatio-temporally joining locations with the same environmental covariates as described for the second-order selection analysis. Specifically, we included slope (linear and quadratic effect) as a proxy of topographic variability; TCD and CHM as measurements of the horizontal and vertical structure of the forest canopy, respectively; the density of COI (dCOI) as a proxy of functional anthropogenic disturbance; and the monthly species richness of fruiting plants (r-berry) as a proxy of food resources. We excluded EVI because the resolution was too coarse (250 m) for the analysis. To further understand the link between the selection of high-quality resources and the avoidance of human-derived risk, we again included an interaction term between resource availability and anthropogenic disturbance. All the covariates included in the final model were also tested for collinearity (Pearson correlation coefficient $|r| \leq 0.6$; Figure S2.4). Finally, individuals were treated as random slopes in the model with respect to anthropogenic disturbance to account for among-individual variability (Gillies *et al*., 2006).

We finally mapped the relative probability of selection of a given location as a resting site, based on a model including all covariates that were significant in the full model (i.e. the most parsimonious model, also based on AIC differences; Hosmer Jr, Lemeshow, & Sturdivant, 2013). We validated the predictive ability of the CLR model by 10-fold cross-validation (Boyce *et al*., 2002), training our model iteratively on $k-1$ data sets, validating it on the remaining test set and testing the model performance of spatially explicit predictions using Spearman's rank correlation coefficient.

Results

Home range selection (second-order)

The final data set we based the second-order selection analysis upon included GPS locations at 6-hour intervals from 12 animals (eight females and four males), for a total of 21 animals-year (out of 44 animal-year). At the population range, brown bears selected home ranges in steeper terrain, at sites with higher productivity and fruit diversity. However, bears traded off the selection of high-quality food against functional human disturbance avoidance. Specifically, habitat quality and productivity were the predictors with the largest effect size for most months (b_{EVI} = +0.545 to +1.028, $P < 0.001$; Table 1). Topographical variability was also an important predictor, as bears selected for steep areas (b_{Slp} = +0.331 to +0.612, $P < 0.001$; Table 1), but avoided extreme slope values in

Table 1 Results of the fitted generalized linear models used to assess brown bear habitat selection at the second-order of selection for each month of the active season (from May to October, April was excluded for the lack of variability in species richness of fruiting plants)

	Coefficients (95% CI)					
	Model					
	May	June	July	August	September	October
Slope	0.612*** (0.536 to 0.688)	0.486*** (0.403 to 0.568)	0.576*** (0.495 to 0.657)	0.538*** (0.463 to 0.612)	0.331*** (0.265 to 0.398)	0.495*** (0.418 to 0.572)
Slope^2	−0.086*** (−0.126 to −0.046)	−0.054* (−0.098 to −0.010)	−0.178*** (−0.226 to −0.129)	−0.171*** (−0.216 to −0.125)	−0.029 (−0.067 to 0.010)	−0.171*** (−0.219 to −0.122)
Enhanced Vegetation Index	0.565*** (0.498 to 0.632)	0.545*** (0.459 to 0.631)	1.028*** (0.944 to 1.112)	0.874*** (0.795 to 0.952)	0.582*** (0.514 to 0.650)	0.940*** (0.857 to 1.022)
dCOI	−0.587*** (−0.681 to −0.493)	−0.500*** (−0.603 to −0.396)	−0.798*** (−0.912 to −0.684)	−0.586*** (−0.678 to −0.494)	−0.767*** (−0.871 to −0.663)	−0.601*** (−0.696 to −0.505)
Berry richness	0.106** (0.052 to 0.161)	0.288*** (0.228 to 0.349)	0.170*** (0.104 to 0.236)	−0.012 (−0.071 to 0.046)	0.241*** (0.184 to 0.299)	0.086* (0.026 to 0.147)
dCOI:Berry richness	−0.027 (−0.110 to 0.056)	−0.149** (−0.232 to −0.065)	−0.088 (−0.192 to 0.016)	−0.116* (−0.202 to −0.029)	−0.086 (−0.176 to 0.003)	−0.176** (−0.265 to −0.087)
Constant	−11.876*** (−11.952 to −11.800)	−11.922*** (−12.013 to −11.830)	−12.109*** (−12.205 to −12.014)	−2.904 (−7.454 to 1.645)	−11.933*** (−12.012 to −11.853)	−10.036*** (−12.662 to −7.410)
Observations	106 058	84 793	100 506	102 810	113 528	94 921

The explanatory variables, parameter estimates, 95% confidence intervals and *P*-values are reported for each monthly model. At the bottom, the number of observations is reported (from a total of 21 animals-year).

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

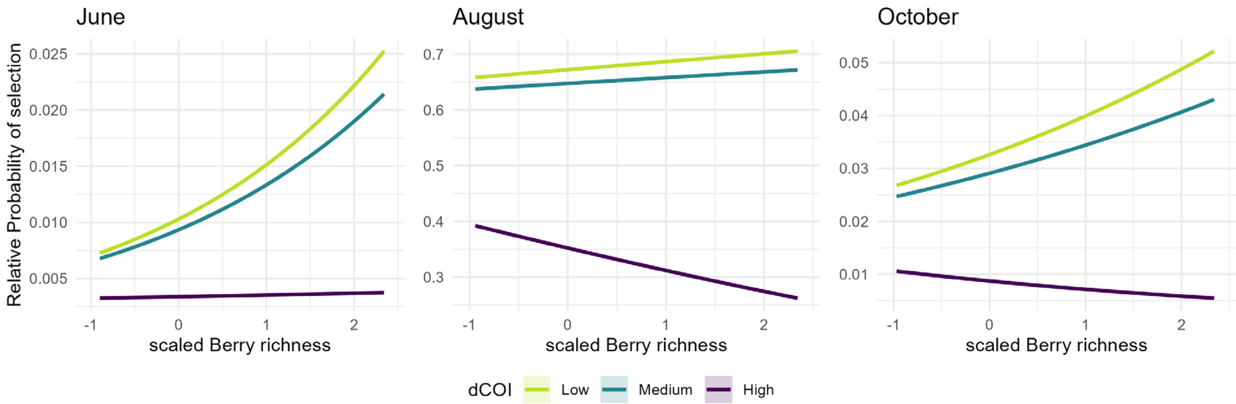

Figure 2 Monthly plots with the relative probability of selection by bears of berry richness (*r-berry*) estimated at three distinct levels of functional disturbance density (*dCOI*), which are indicated by different regression lines. Only the monthly models with a statistically significant interaction term (*dCOI:r-berry*) are reported.

certain months ($b_{Slp\textasciicircum 2}$ = −0.054 to −0.178 when there is a significant relationship, $P < 0.05$ to $P < 0.001$; Table 1). In June, August and October (Table 1; Table S4), the positive selection of species richness of the fruiting plants by bears was inversely dependent on human disturbance increase ($b_{dCOI:r\text{-}berry\text{-}}$ = −0.116 to −0.176, $P < 0.05$ to $P < 0.01$; Fig. 2, Table 1). In May, July and September when the interaction was not significant (Table S4), bears selected for areas with high species richness of fruiting plants ($b_{r\text{-}berry}$ = +0.106 to +0.2417, $P < 0.01$ to $P < 0.001$; Table 1) and avoided high density of functional disturbance (b_{dCOI} = −0.587 to −0.798, $P < 0.001$; Table 1).

Resting site selection (third-order)

Through the spatiotemporal clustering of GPS bear locations, we were able to classify a total of 557 resting sites. Bears primarily selected their resting sites in areas with a low density of functional anthropogenic disturbance (b_{dCOI} = −0.752, $P < 0.001$; Fig. 3, Table 2), more so than any other

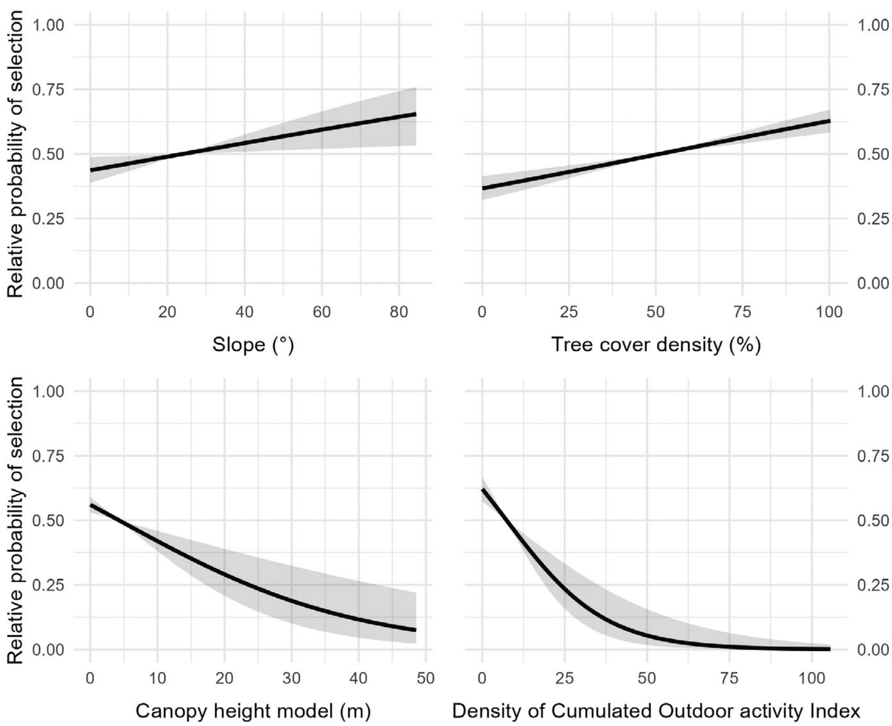

Figure 3 Fitted regression lines with standard error showing the empirical association between resting site use and the significant environmental predictors, estimated using conditional logistic regression. The regression coefficients are derived from the best-fitting model (i.e. with slope, tree cover density, canopy height model and density of COI).

Table 2 Results of the fitted mixed-effects conditional logistic regression used to assess brown bear selection of resting sites

Explanatory variable	Coefficient	CI (95%)	*P*-value
Slope	0.241	0.065–0.417	<0.01
Slope^2	−0.067	−0.159 to 0.026	>0.05
Tree cover density	0.412	0.244 to 0.581	<0.001
Canopy height model	−0.308	−0.458 to −0.158	<0.001
dCOI	−0.752	−1.083 to −0.421	<0.001
Berry richness	0.046	−0.124 to 0.215	>0.05
dCOI:Berry richness	−0.016	−0.266 to 0.234	>0.05

The explanatory variables, parameter estimates (conditionally standardized), 95% confidence intervals and *P*-values are reported.

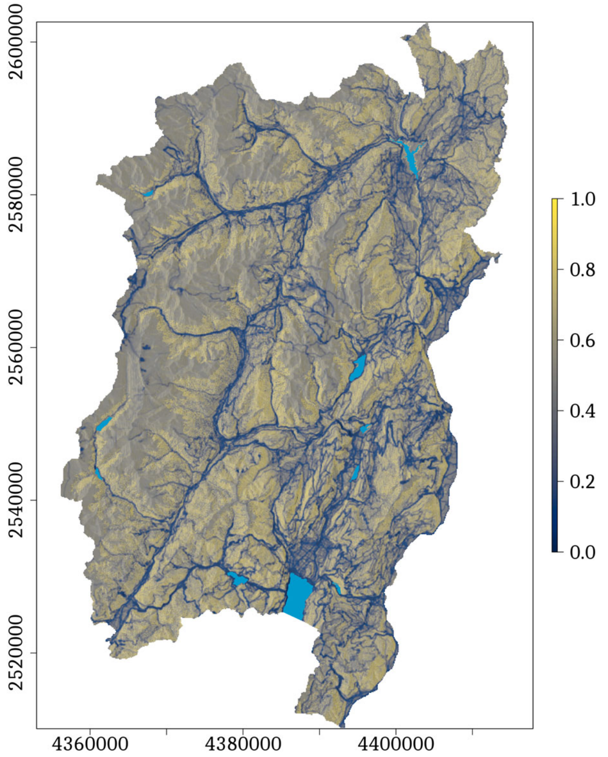

Figure 4 Map of the predicted relative probability of use as resting location by brown bears in Western Trentino. The prediction is based on the estimated coefficient values from the mixed-effects conditional logistic regression model. The map has a resolution of 20 m pixel size.

spatial covariate. Bears also selected for resting sites under higher horizontal ($b_{TCD} = +0.412$, $P < 0.001$; Fig. 3, Table 2) and lower vertical canopy cover ($b_{CHM} = -0.308$, $P < 0.001$; Fig. 3, Table 2). Slope was positively selected as a linear effect ($b_{Slp} = +0.241$, $P < 0.01$; Fig. 3, Table 2), but not when included as a quadratic term ($b_{Slp\text{\^{}}2} = -0.067$, $P > 0.05$; Table 2). Importantly, the availability of resources did not significantly affect the selection of resting sites, neither as an additive factor ($b_{r\text{-}berry} = +0.046$, $P > 0.05$; Table 2) or in interaction with human-derived disturbance ($b_{dCOI:r\text{-}berry} = -0.016$, $P > 0.05$; Table 2). The spatial prediction (Fig. 4) was obtained including only the significant terms, namely Slp, TCD, CHM and dCOI (Fig. 3). The k-fold cross-validation of such model provided consistent spatial predictions of the relative probability of resting site use (average Spearman's correlation coefficient: $r = +0.98$, $P < 0.001$).

Discussion

Our results indicate that brown bears in the Alps try to reduce human-derived risk exposure by modulating their behaviour at different ecological scales and annual physiological phases. By analysing their movement data in combination with recently developed covariates, we showed that bears weighed the selection for areas with high-quality food against high functional human disturbance avoidance, particularly during late hyperphagia, supporting hypothesis (i). By analysing the distribution of resting sites, we also found that the overall perception of risk influenced fine-scale selection more than available resources, supporting a security-food trade-off strategy (hypothesis (ii)). These results suggest that humans, as the largest predator and competitor in the Alpine ecosystem, played a primary role in modifying space use, resting patterns and foraging behaviour of the brown bear. In a community ecology framework (Chapron & López-Bao, 2016), the ecological niche (*sensu* Hutchinson, 1957) of the bear was potentially reduced as a result of both risk perception and habitat competition.

Risk perception drives the selection of space, resources and resting sites in Alpine bears

Previous studies (Preatoni *et al.*, 2005; Peters *et al.*, 2015) have shown that the Alpine brown bear tends to avoid proximity to human settlements and infrastructure (i.e. a structural effect). By including human mobility data, it has been recently demonstrated that functional anthropogenic disturbance primarily drives selection within the home ranges (Corradini *et al.*, 2021a). Our results complement those findings by showing that bears, within their population range, selected for home ranges with high habitat quality but low anthropogenic disturbance, independently of annual physiological phases. In particular, human mobility offered an ecologically meaningful proxy of perceived risk ('landscape of fear'; Gaynor *et al.*, 2019) for bears in the Alpine region. Rugged areas were also selected as likely less disturbed by humans (Martin *et al.*, 2010).

The presence of people in the environment likely induced bears to balance risk with access to areas with high-quality food, that is, higher richness of fruiting plants, throughout the active season. During hyperphagia, when highly caloric food is needed for accumulating fat for winter denning (i.e. particularly important for the reproductive capacity of females; Robbins *et al.*, 2012), fleshy fruits such as berries represent an important food source for bears (Ciucci *et al*., 2014). Bears selected areas with high fruit richness, likely because they provide predictable and profitable food sources. However, when the perception of anthropogenic risk was high, bear selection was less influenced by fruit richness. This indicates a behavioural response to humans (i.e. risk effects; Creel & Christianson, 2008), resulting in decreased foraging efficiency for fleshy fruits (Fig. 2). While bears would likely redirect feeding towards other energetic sources, being a wide spectrum omnivore with plastic trophic behaviour (Coogan *et al*., 2018), this shift in fruit consumption could potentially have cascading impacts on seed dispersal services and plant regeneration processes (García-Rodríguez *et al*., 2021). Alternatively, bears may be occasionally attracted to high-quality food sources in proximity to human settlements during periods of high nutritional demand, potentially leading to ecological traps (Penteriani *et al*., 2018).

Previous research on bear activity patterns (Tattoni *et al*., 2015; Oberosler, Tenan, & Rovero, 2020), assessed by systematic camera trapping, showed a reduced daytime activity alongside increasing human presence. Because shifting areas of use is an important mechanism by which animals can decrease the risk of interaction with humans (Tablado & Jenni, 2017), periods of inactivity such as resting, when animals have a reduced capacity to detect changes in their surroundings and cope with risky situations, can be particularly vulnerable (Anderson, 1998). For this reason, it is expected that resting site selection is first and foremost determined by risk perception (i.e. 'where to sleep'; Lima *et al*., 2005), as observed for example in other large mammals (e.g. African elephant; Wittemyer *et al*., 2017; or wild boars; Fradin & Chamaillé-Jammes, 2023). In our research, we showed that risk aversion influenced the resting site selection by brown bears: not only did individuals select sites with reduced recreational human use but also on steeper terrain and with denser canopy cover. Resting sites were therefore chosen as both inaccessible (i.e. more rugged terrain; Martin *et al*., 2010) and concealed (possibly providing thermal comfort too; Lima *et al*., 2005) to humans, hence likely perceived as safer. Further, bears prioritized individual security over food intake during resting (Cristescu, Stenhouse, & Boyce, 2013), as proximity to productive feeding areas did not affect site choice.

The predictive map showed that, in our study area, large sections are currently unsuitable for resting sites, because of exposure to disturbance and high fragmentation. While vast suitable contiguous areas are found to the west of the study area, greater fragmentation and lower suitability characterize the east, especially the southern sector, limiting the availability of resting sites (Fig. 4). More secluded, steep and forested areas could provide shelter, suggesting that bears can currently locally segregate from humans at times of higher disturbance (i.e. daytime). However, limited areas suitable for resting, combined with concurrent limits on habitat connectivity (Peters *et al*., 2015) and low local habitat suitability (Corradini *et al*., 2021a), may provide additional hurdles to individual space use, and consequently population range expansion beyond the reintroduction range (Tosi *et al*., 2015).

Humans potentially shape bear's niche

The ecological niche describes the habitat and factors that locally determine the set of conditions required for the persistence of the species (i.e. the realized Grinnellian niche; Hirzel & Le Lay, 2008). We recognize that numerous definitions of ecological niche exist (see review from Pocheville, 2015), enumerating many 'dimensions' defining its space (Polechová & Storch, 2008). We decided to refer to 'niche' in the broadest sense of 'species persistence', as pointed out by Pocheville (2015, pp. 575): '*[. . .] its [niche] multiple meanings all revolve around the Darwinian view of ecosystems that are structured by the struggle for survival*'.

Humans are functioning as the main predator and space competitor of bears in the Alps, driving their adult survival (Tenan *et al*., 2016), and space distribution (Peters *et al*., 2015; Corradini *et al*., 2021a; this work). Our findings suggest that the spatial variation in human-related risk perception (Gaynor *et al*., 2019), expressed as human functional disturbance (Corradini *et al*., 2021a), influenced bear space, resource and resting site selection, similar to what one would expect in a community ecology framework (Chapron & López-Bao, 2016). To persist in the landscape, animals must alter their realized niche in the presence of interspecific interactions (i.e. predation and competition; Hutchinson, 1957). In the Alps, bears may have altered their realized niche due to the competition for space with humans. These types of 'niche restrictions' due to humans may have a cumulative effect with other human impacts. Humans are the world's primary ecosystem engineers (Root-Bernstein & Ladle, 2019) and their 'footprint' (e.g. urbanization, climate change; Boivin *et al*., 2016) goes far beyond competition and predation. Anthropogenic impact thus changes the multidimensional space of favourable conditions of species (i.e. Hutchinson, 1957) even before ecological interactions are taken into account.

Implications for coexistence

Following the conceptual framework proposed by Chapron & López-Bao's (2016), the level of coexistence between humans and bears in the Alps can be considered 'weak': human competitive ability remains high due to lack of effective protection (human-caused mortality drives adult survival; Tenan *et al*., 2016), but behavioural adaptations and plasticity of bears (this study) and adequate human practices (i.e. bear–human conflict prevention; PACOBACE, 2010; Groff *et al*., 2022) increase niche differentiation. However, some degree of niche overlap between the two species emerges, and such overlap is potentially expanding, touching upon farming activities (Peters *et al*., 2015) and human mobility (Corradini *et al*., 2021a; this work; see also Passoni, Coulson, & Cagnacci, 2023). Since population redistribution over a larger area is unlikely because of species biological traits (such as female philopatry) and habitat limitations (i.e. lack of connectivity, Peters *et al.*, 2015; Corradini *et al.*, 2021b), bear mobility and presence could increasingly clash with human activity. In some instances, this overlap can cause individual brown bears to exhibit behavioural responses that escalate to harmful attacks on humans (Bombieri *et al.*, 2019). While such incidents are uncommon, there have been eight reported attacks in the Central Alps over the past decade, one of which was lethal in April 2023 (Ufficio Stampa della Provincia Autonoma di Trento, 2023). Current measures to limit the probability of human-bear direct interaction include preventing access to anthropogenic food to avoid the emergence of food conditioning, reducing confident behaviour through aversive conditioning, and in extreme circumstances, the legal removal of bears for conflict management (ISPRA–MUSE, 2021). Lack of legal responses may result in retaliatory poaching, potentially affecting population growth and jeopardizing the long-term viability of the Alpine-Dinaric brown bear meta-population (Kaczensky *et al.*, 2012).

In this context, a shift from a weak to a strong level of coexistence could be achieved by further reducing occurrences of human-bear direct competition (from human-induced mortality to high tolerance of predators; Chapron & López-Bao, 2016) and implementing adequate human practices to increase niche differentiation. Legislative measures can be put into effect to restrict or control retaliation killing. In parallel, educational and outreach programmes can contribute to fostering greater tolerance towards bears, especially while the population is re-establishing at the edge of highly anthropic areas (Passoni, Coulson, & Cagnacci, 2023). On the other hand, understanding how bears perceive risk can help guide practices to increase niche differentiation. Using the spatial predictions of this study (Fig. 4), specific measures to limit anthropogenic disturbance in situations of vulnerability for bears, such as when resting and during sensitive annual physiological phases, could be implemented. For example, modulating the spatio-temporal overlap between humans and bears could potentially mitigate the risk of conflict. Human access rules have been successfully implemented at different degrees in a variety of socio-ecological contexts. These include extensive wilderness areas, such as Bear Management Areas (BMAs) in Yellowstone National Park (Coleman *et al.*, 2013), or temporary limitation of human activities in more human-dominated contexts, for example, closure of bear breeding areas in Spain (Planella *et al.*, 2019), or motorized access controls in Canada (Proctor *et al.*, 2020), whereas in the Pyrenees, hunting regulations were recently implemented to reduce disturbance and conflict (Farcaza, 2022). Conversely, potential areas of conflict risk could be identified through spatial prediction of connectivity corridors and the dispersal of bears into new, uncolonized areas (Ditmer *et al.*, 2023). This could inform the implementation of localized management measures (such as the provision of bear-proof recycle containers) and targeted education programs (Passoni, Coulson, & Cagnacci, 2023).

If embraced by the local community, without being seen as a restriction on freedom of movement, some of these strategies can reduce human-bear niche overlap and thus conflict potential. Indeed, the effectiveness of these measures is specific to the landscape structure and its customary fruition by humans, which in turn is often linked to the cultural-historical context. For example, a very dense network of trails together with the traditional fruition of natural resources managed at the municipality scale (e.g. wood harvesting, mushroom picking) may limit the effective implementation of restricted access areas. Nevertheless, the knowledge of spatio-temporal opportunities to decrease human–bear conflicts via continued bear movement and behaviour monitoring and modelling offers opportunities for sets of suggestions to increase bear awareness and induce safer human behaviours; while also underpinning the application of preventive legal measures to manage bear behaviour.

When communicated positively and effectively, also highlighting opportunities for living with bears, co-existence suggestions can be accepted by tourists and residents alike (Abrams *et al.*, 2020; Passoni, Coulson, & Cagnacci, 2023). The bear is an iconic mammal that can promote nature-oriented tourism (Tattoni, Grilli, & Ciolli, 2017). High levels of coexistence in human-dominated landscapes are difficult to achieve (Morales-González *et al.*, 2020), but if reasonable and targeted mitigation measures are taken, brown bears could finally thrive in the Alps for many years to come.

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Author contributions

AC, DF, LP, NR, CT, MC and FC conceived the ideas and designed methodology; AC, DF, NB and CG collected the data; AC and DF analysed the data; AC and FC led the writing of the paper. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Animal capture details and protocols.

Data S2. Description and correlation analysis of spatial covariates.

Table S2.1. Selected spatial covariates used in the multi-scale selection analysis.

Figure S2.1. Monthly variation (i.e., during the active season for bears) in the Enhanced Vegetation Index (EVI) over the study area.

Table S2.2. Species commonly eaten, or considered edible, by brown bears (based on current available literature on bear feeding habits) among those identified as available in the Alps.

Figure S2.2. Monthly availability (i.e., during the active season for bears) of high-quality fruit richness from plants commonly eaten, or considered edible, by brown bears (*see* Table S2.2 for the detailed list of species).

Figure S2.3. Correlation matrix with the Pearson correlation coefficients between each variable chosen for the second-order selection analysis.

Figure S2.4. Correlation matrix with the Pearson correlation coefficients between each variable chosen for the third-order selection analysis.

Data S3. Field validation of remotely identified resting sites.

Figure S3. Graphical representation of the spatiotemporal cluster analysis used to identify resting sites.

Data S4. Model comparison (second-order selection analysis) by the analysis of deviance.

Table S4. Intra-monthly comparison of models via analysis of deviance.

