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Animal movements occurring during COVID-19 lockdown were predicted by connectivity models

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Article impact statement: Connectivity of wildlife habitat increases during reduced human mobility.

Abstract

Recent events related to the measures taken to control the spread of the Coronavirus (SARS-CoV-2) reduced human mobility (i.e. anthropause), potentially opening connectivity opportunities for wildlife populations. In the Italian Alps, brown bears have recovered after reintroduction within a complex anthropogenic matrix, but failed to establish a metapopulation due to reduced connectivity and human disturbance (i.e. infrastructure, land use, and human mobility). Previous work from Peters et al. (2015, Biol. Cons. 186, 123-133) predicted the main corridors and suitable hot spots for road network crossing for this population across all major roads and settlement zones, to link most suitable habitats. Bears used the identified hot spots for road network crossing over the years, but major barriers such as main motor roads were not overcome, possibly due to functional anthropogenic disturbance, specifically human mobility. By analyzing 404 bear occurrences reported to local authorities (as bear-related complaints) collected between 2016 and 2020 (March 9th - May 18th), hence including the COVID-19 related lockdown, we tested the effect of human presence on brown bears' use of space and hot spots for road network crossing. Animals occupied human-dominated spaces and approached hot spots for crossing at a higher rate during the lockdown than in previous years, suggesting that connectivity temporarily increased with reduced human mobility for this population. As a result of their increased use of hot spots, bears expanded their use of suitable areas beyond the population core area. Movement of animals across structural barriers such as roads and human settlements may therefore occur in absence of active disturbance. We also showed the value of predictive models to identify hot spots for animal barrier crossing, the knowledge of which is critical when implementing management solutions to enhance connectivity. Understanding the factors that influence immigration and emigration across metapopulations of large mammals, particularly carnivores that may compete indirectly with humans for space or directly as super-predators, is critical to ensure the long-term viability of conservation efforts for their persistence. We argue that dynamic factors such as human mobility may play a larger role than previously recognized.

Keywords: *Ursus arctos*; Anthropause; Human mobility; Connectivity; Wildlife road crossing; Anthropogenic disturbance.

1. Introduction

Several studies have shown that permanent human land use, infrastructure and disturbance affect mammalian behaviour by limiting movement (Tucker et al., 2018), conditioning habitat selection (Prokopenko et al., 2017), and shifting activity cycles (Gaynor et al., 2018). Increasing evidence shows that human presence may induce stronger responses at different spatio-temporal scales than infrastructural barriers (Corradini et al., 2021; Nickel et al., 2020). However, it has so far proven difficult to disentangle the effects of these two, often co-occurring, components of human disturbance.

Recently, the lockdown enforced to contain the spread of the Coronavirus (SARS-CoV-2) revealed the consequences of an abrupt interruption of human mobility on ecosystems (i.e. "anthropause", Rutz et al., 2020). Hence, unprecedented insights into how human activities influence animal behaviour may emerge (Bates et al., 2020; Diffenbaugh et al., 2020; Bates et al., 2021). Human presence has been completely removed from certain landscapes only under extreme circumstances (e.g. disease control, radioactive contamination, or mass socio-geographic shifts). These tragedies inadvertently created the context to study the effects of such human interventions on natural ecosystems (Bowen et al., 2007; Deryabina et al., 2015; Navarro and Pereira, 2021). The anthropause may represent one of those.

In Italy, one of the countries first affected by the SARS-CoV-2, the nation-wide lockdown lasted from March 9th to May 18th 2020, the longest and most stringent enforced in Europe (based on the Stringency Index; Hale et al., 2021). The lockdown remained strict until May 3rd (i.e. no outdoor activity was allowed, people were confined at home within a radius of 200m; mean Stringency Index = 90.78), and mobility was significantly limited until May 18th (i.e. interregional travelling prohibited, most of the commercial activities closed; mean Stringency Index = 63.55) (Figure S1). These confinement measures were enforced through active police control. People could temporarily access their properties and belongings, but only when strictly necessary and accompanied by a written justification. In these very tragic and unprecedented circumstances, wildlife witnessed unexpected 'competitor/predator removal' and uncommon behaviours have been observed, for example, an increase of urban or diurnal observations of opportunistic species (Manenti et al., 2020), although experimental evidence on cryptic species in wilder areas is still lacking.

In the Eastern Italian Alps, a highly anthropized region, a brown bear (*Ursus arctos*) population has re-established after reintroduction (Mustoni et al., 2003), but has so far failed to spatially expand its range beyond the release area and rejoin the Alpine-Dinaric metapopulation. The region is characterized by dense human infrastructure in the low valleys, which has been considered one of the main reasons for reduced connectivity (Kaczensky et al., 2012). Based on habitat selection models, previous work predicted the most suitable areas and relative main connectivity corridors for bear at the regional scale, identifying hot spots for road network crossing (Peters et al., 2015). Bears rarely used the identified hot spots over the years, because major barriers such as heavily trafficked roads were not overcome. This can be explained by the functional anthropogenic disturbance hypothesis, where human presence and mobility would restrain bear movements more than infrastructure *per se* (Corradini et al., 2021).

The unexpected circumstances of COVID-19 prompted us to investigate the effects of the lockdown on brown bears by analyzing, with a quasi-experimental design (Rutz et al., 2020), their space use with respect to permanent human infrastructure, while active human disturbance was temporarily reduced. We hypothesised that, in a time of low human mobility, landscape permeability for bears would increase. We tested this hypothesis by assessing three predictions: (i) bears used human-dominated spaces (measured as human property damage) more frequently than in the previous years due to lack of human active disturbance and (ii) bears approached the connectivity hot spots previously identified by Peters et al. (2015), to a significantly higher extent than in the previous year ; (iii) finally, as a consequence of this increased use of hot spots to overcome human infrastructure, we predicted an expansion of bears over use of the suitable range.

2. Materials and methods

2.1 Study area

The study was conducted in the province of Trento (or Trentino), Italy (46°26′44″N, 11°10′23″E), a rugged mountain region of 6,200 km^2 in the Central-Eastern Alps. This Alpine biogeographic region also encompasses human-dominated Alpine valleys (87 inhabitants/km^2) characterized by a large infrastructural network of roads, railways, forestry roads, and trails, which make most of the territory accessible to humans. About 500,000 people live in the province, with an annual tourist influx nearly ten times as much (Ispat, 2020). A bear population of about 82-93 bears persists in the area (Groff et al., 2020) as a result of a reintroduction program implemented between 1998 and 2002 (Mustoni et al., 2003). Despite steady population growth and a substantial increase in the occupied area following reintroduction (Groff et al., 2020), the Alpine bear population remains genetically isolated and the Alpine-Dinaric metapopulation is not yet restored due to lack of connectivity (Kaczensky et al., 2012).

2.2 Bear occurrence reports and damage events (prediction (i))

To evaluate whether bear use of human-dominated spaces was influenced by human presence, we considered bear-related damages or occurrences that are typically very noticeable and easy to identify (Figure S2). As part of a compensation scheme initiated after the reintroduction program, people are encouraged to report any damage or observations to local authorities through an active 24/7 hotline (PACOBACE, 2010). Despite a concerted effort to mitigate damages over the last 20 years and a steady increase in the prevention measures put in place (Groff et al., 2020), some properties remain vulnerable to bear attack, especially on the edges of the population range. For this study, we collected all confirmed bear occurrences (bear-related damages, sightings, and signs of presence) reported to local authorities in the province of Trento between 2016 and 2020. Even in 2020, occurrences and damages could be discovered during permitted activities outside the house (e.g., animal care, garbage disposal, agricultural activities), then, according to the procedure in place, reported by telephone and registered after an inspection by local authorities (i.e. Forestry Corps; PACOBACE, 2010). For each record we obtained: date, event (i.e. damage, sighting, or sign of presence), target (only when damage was reported, i.e. beehive, garbage, building, livestock, orchard, and poultry; Table S1), geographic position (when available), and location reliability (i.e. 500 m; 500–100 m; 100 m accuracy). For each year (2016–2020), we only considered events that occurred from March 9th to May 18th, corresponding to the 2020 lockdown. To test prediction (i), we selected *only damage* events as a proxy for bear use of permanent human-dominated spaces (Table S1) and performed a series of tests comparing the number of complaints that occurred in 2020 against any other year. We did so by fitting a Generalized Linear Model (GLM) with a Poisson error distribution for every category of damage, using year as the predictive variable and number of damages as the response variable. We linearly re-scaled damage counts dividing by the number of bears in the population for that year and multiplying by the estimated bear population size in 2020 to simulate that the population remained constant. For 2016–2019, we used estimates based on genetic Capture–Mark–Recapture from opportunistic sampling (Groff et al., 2020), and for 2020, we used estimates based on probabilistic population growth projections (ISPRA–MUSE, 2021).

Specifically, the bear population was estimated at 44 (38-61) individuals in 2016, 53 (46-71) in 2017, 58 (52-72) in 2018, 75 (66-97) in 2019, and 80 (67-95) in 2020. We also compared the number of bears in the last five years to evaluate whether a significant increase in abundance was observed. To this end, we used bootstrapping (n = 999 iterations) to test for population growth while allowing for uncertainty in the estimates. We did so by randomly sampling the number of bears from a uniform distribution for each year, choosing any possible estimate within the confidence interval. Thus, for each iteration, we tested if there was a significant increase in abundance between 2020 and any other year (2016-2019).

2.2 Connectivity model and use of hot spots for road network crossing (prediction (ii) and (iii))

To evaluate whether bear use of hot spots for road network crossing was influenced by human presence, we considered a previously developed, spatially explicit connectivity model stemming from a resource selection function (Table S2; Peters et al., 2015). Using GPS data from individual bears and a set of ecologically meaningful, remotely sensed habitat information, the authors identified patches of high-quality suitable habitat. The movement corridors were then estimated as the least-cost path between the most suitable habitat patches within the province of Trento. As a result, the authors identified hot spots for road network crossings of predicted paths between preferred habitat patches and classified them into three categories based on local density of crossings (i.e., low -, medium -, and high density; Peters et al., 2015). To test prediction (ii), we considered *all types* of bear occurrences (i.e. damages, sightings, and signs of presence) located outside preferred habitat patches and reported with an accuracy greater than 500 m. We compared bear occurrences recorded in 2019 and 2020 only (March 9th - May 18th), as these were geo-referenced, and referred to years with likely stable population size. We then measured the euclidean distance between each observation and the nearest hot spot for road network crossings (true events, 1), and compared the distribution of distances with that obtained for 1,000 random locations (random draw, 0), extracted in the concave hull defined by the vertices of the most suitable areas (Gombin et al., 2020). To this end, we excluded the observations at the margin of the study area, as hot spots for road network crossing were not estimated beyond Trentino (about 1% points). We then fitted a set of Generalized Linear Models (GLMs) with a binomial error distribution of the true/random points in dependence on the proximity to all hot spots (with low -, medium -, and high density of crossings), and to each category of hot spots at a time. We added the year as a fixed term and included an interaction term between year and proximity to hot spots for road network crossing, in each of the four models. All distances were normalized for the analysis by subtracting the mean and dividing by the standard deviation of the model-specific proximity to hot spots distribution. We selected the most parsimonious models using both the Analysis of variance (ANOVA) and the second-order Akaike Information Criterion (AICc). Finally, to test prediction (iii), we used the two-samples Wilcoxon test to compare the distance from the population core area between bear occurrences reported in 2019 and 2020. We performed the analyses on open-source software QGIS 3.4.4 (QGIS Development Team, 2019) and R 3.4.3 (R Core Team, 2017) under Ubuntu 16.04.3 LTS (Canonical Ltd., London, United Kingdom).

3. Results

We collected a total of 404 reports of bear occurrence: 64 in 2016, 59 in 2017, 44 in 2018, 64 in 2019, and 173 in 2020 for the reference period March 9th - May 18th (Figure 1; Table S3 for details). The bear population size increased significantly in 2020 compared to 2016 and 2017 (Table 1 and S4), as also indicated by bootstrapping (Figure S3), whereas the increase was not statistically significant compared to 2019 (Table S4), and with less certainty, to 2018 (Figure S3). We observed a significant increase in reported damage to human properties (i.e. poultry, garbage, building, and beehive) standardised for bear population size in 2020 compared to any other year, except for 2016 (Table 1 and S4), supporting prediction (i). Instead, despite being periodically inspected, targets not in close proximity to human dwellings (i.e., orchard and livestock; Table S1) were not damaged significantly more during the lockdown than in previous years (2016-2019; Table 1 and S4).

The bear occurrences recorded with high spatial reliability outside preferred habitat patches were closer than random to hot spots for road network crossing, irrespective of year, for all four models considering proximity to different categories of hot spots (bAll crossing = -0.59, p <0.001; bLow density = -1.13, p <0.001; bMedium density = -2.40, p <0.001; bHigh density = -2.24, p <0.001; Table 2 and Figure 3; Table S5 and S6). Further, the bear occurrences were significantly more in 2020 than in 2019 in the model considering all categories of hot spots for road network crossing (114 and 30, respectively; bYear(2020) = +1.33, p <0.001; Table 2 and Figure 3), supporting prediction (ii). This relation held for the model including observations in proximity to hot spots of medium density of crossings (bYear(2020) = 2.48, p <0.001; Table 2 and Figure 3), but not for the other models (Table S5). Finally, we found that occurrences in 2020 were reported in areas that were significantly further away from the population core area than in 2019 (W = 123, p = 0.005; Figure 4), indicating an expansion of bears over their suitable range, supporting prediction (iii).

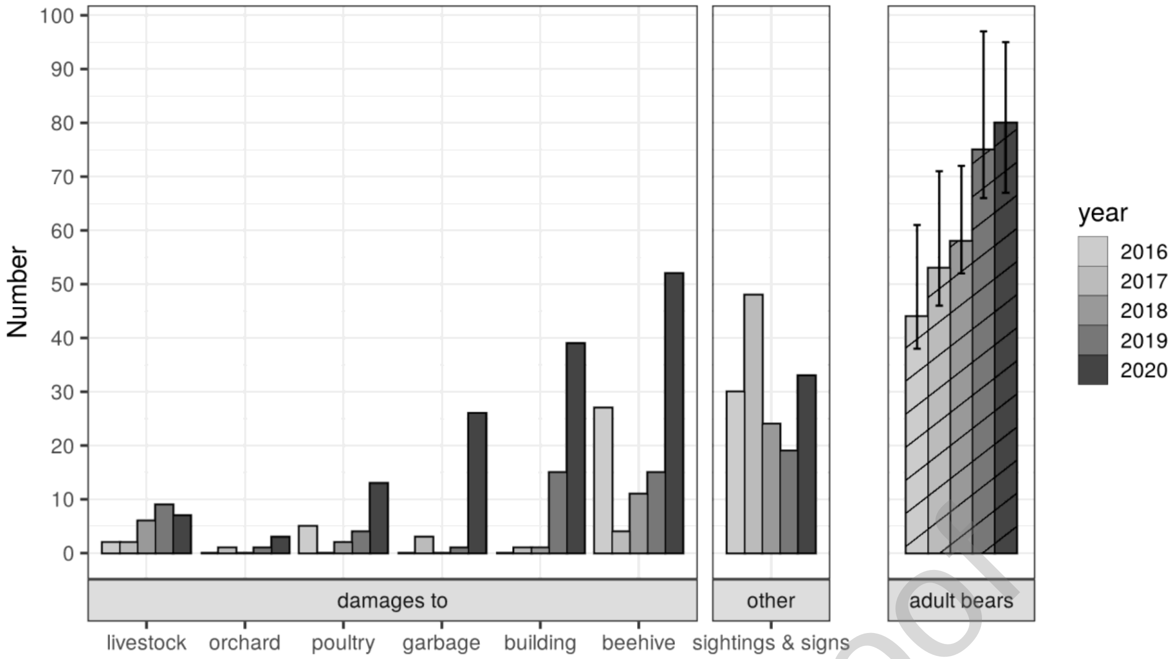

Figure 1 - Recorded occurrences (bear-related complaints classified by damage type, sightings, and signs of presence) , during the period between March 9th and May 18th (time interval of the 2020 lockdown), in the years 2016-2020. Bars referring to successive years are coloured in increasingly darker shades of grey. The estimated number of bears per year, with 95% confidence interval (Groff et al., 2020; ISPRA–MUSE, 2021) is also reported.

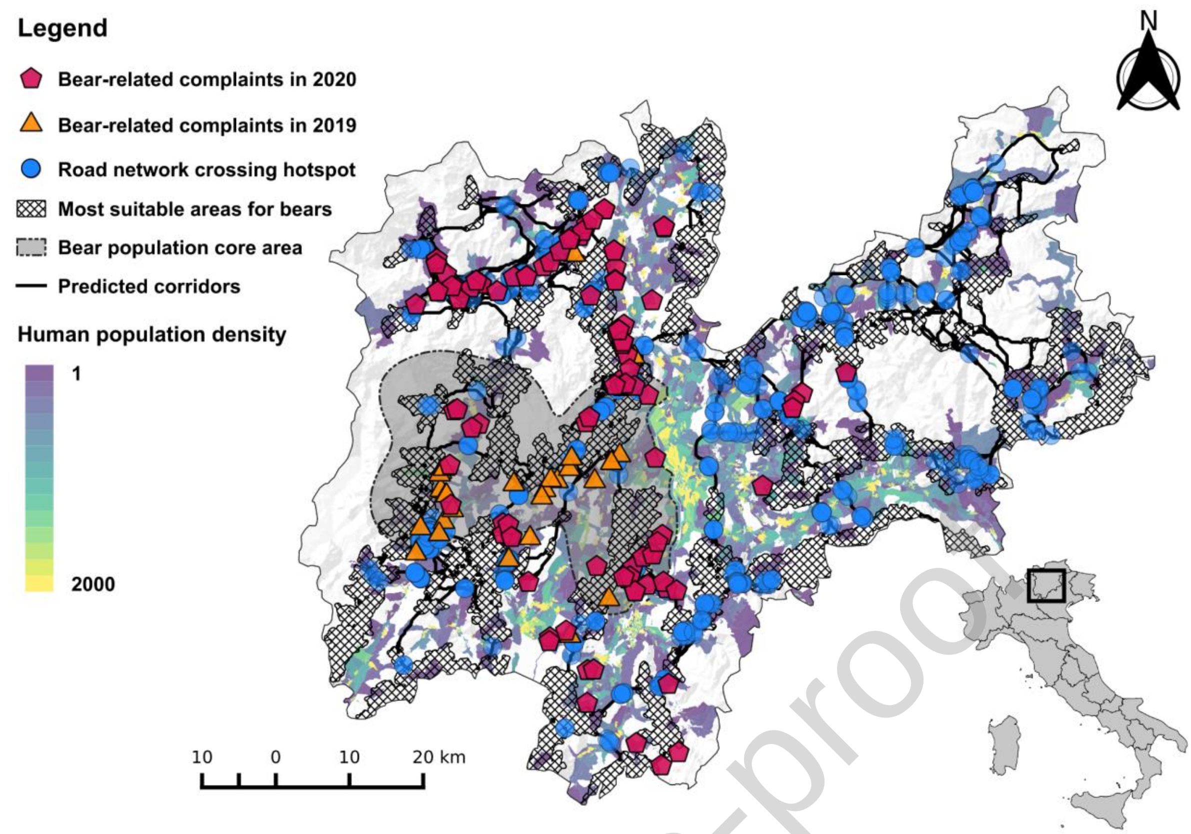

Figure 2 - Recorded bear occurrences (all event types, pentagon for 2020 and triangle for 2019) mapped over the province of Trento, Italy, during the lockdown period of March 9th to May 18th. The predicted most suitable bear habitat (cross-hatching) and relative corridors (continuous lines) identified by Peters et al. (2015), as well as all the hot spots for road network crossing (circle) and the bear population core area (light grey), are shown for reference. The continuous gradient shows the total resident human population density for administrative units (Istat, 2015).

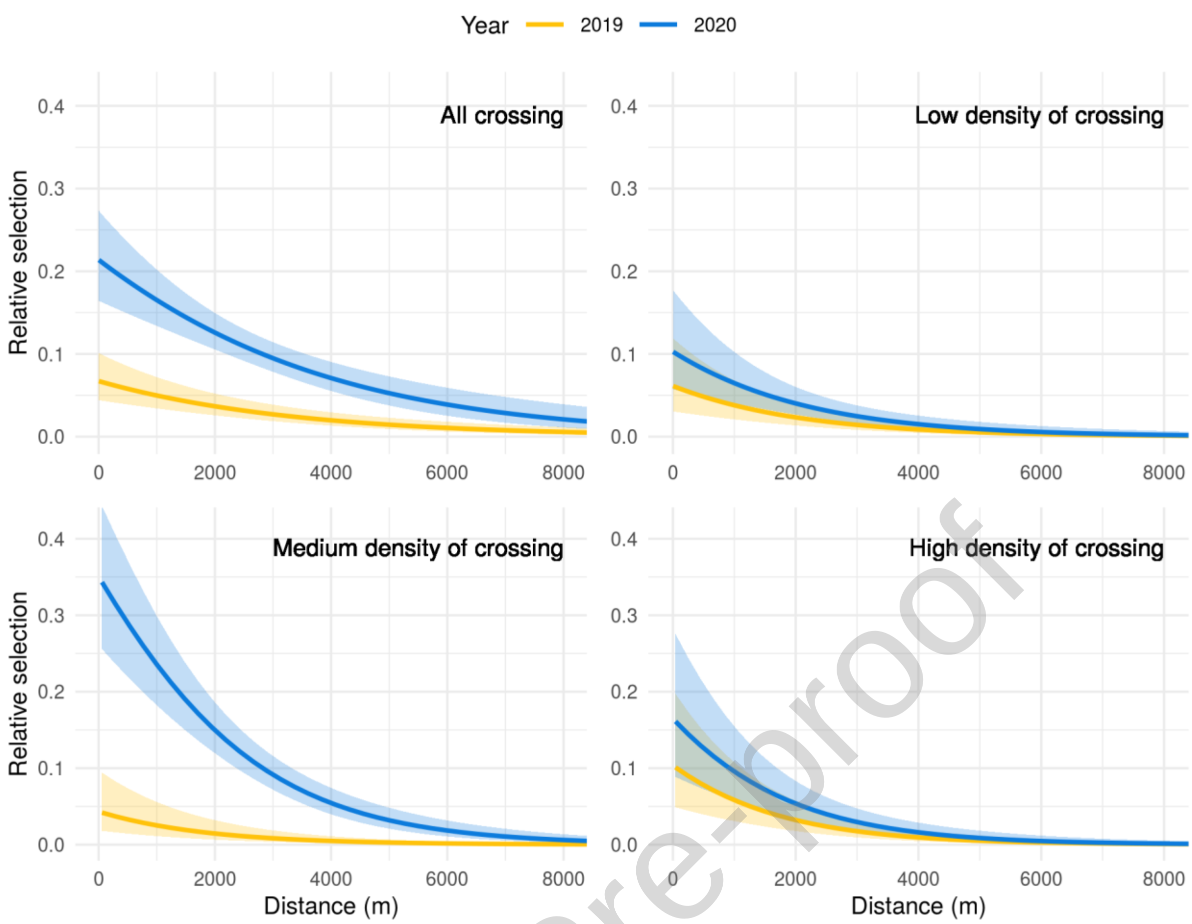

Figure 3 - Fitted regression lines with 95% confidence bands, estimated via Generalized Linear Models, of the empirical relationship between bear space use (as bear occurrences, compared to a random draw) and the proximity to hot spots for road network crossing (all, low -, medium -, and high density) between 2019 and 2020, in the period March 9th and May 18th. We plotted the relative probability of occurrence with respect to proximity to hot spots by year, even when not included in the best model, for comparison purposes. Year was included in the overall model and for proximity to hot spots for medium density of crossings.

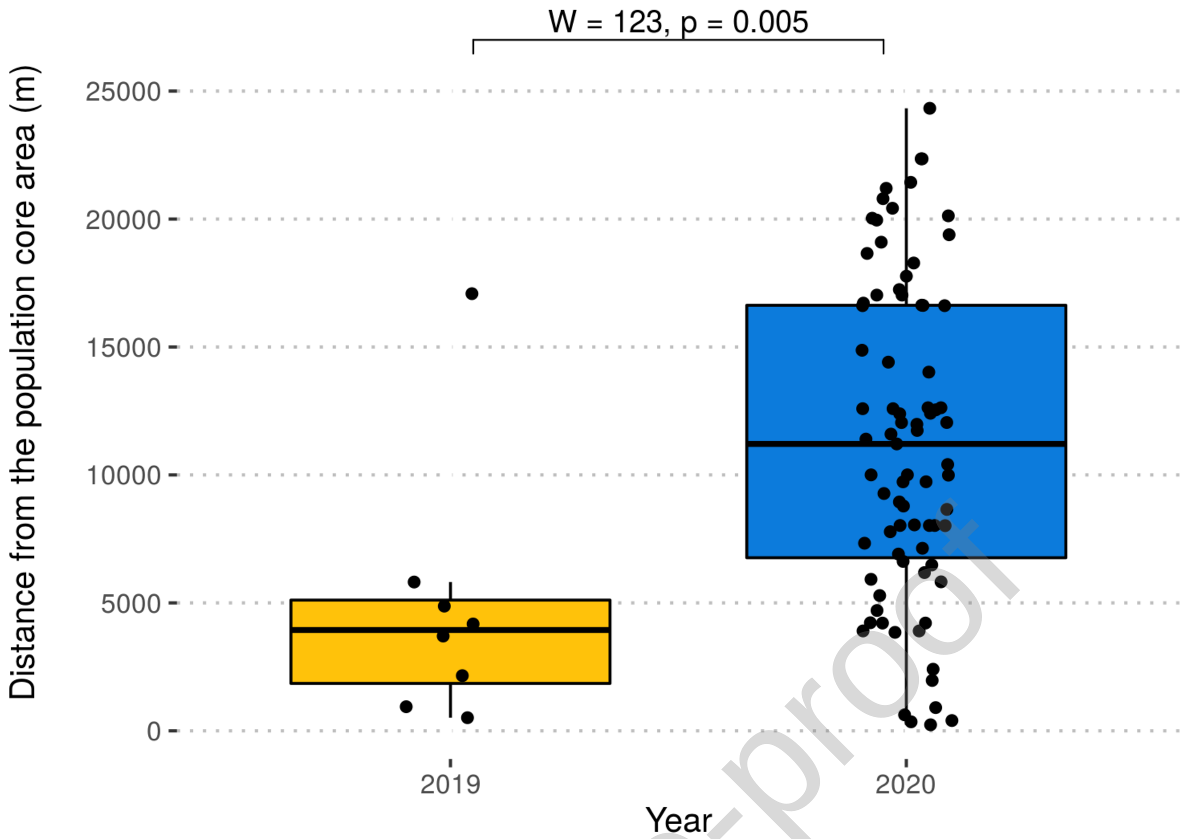

Figure 4 - Proximity of bear occurences to brown bear population core area (Figure 2) in 2019 and 2020, reported during the period March 9th - May 18th. Each dot represents a bear occurrence reported with high spatial reliability (< 500 m accuracy). Above the boxplots: output of the two-sample Wilcoxon test for the distribution.

Table 1 - Results from the Generalized Linear Model with a Poisson error distribution fitted to the number of bear damage complaintss, standardised for bear population size,in dependence on the type of complaint and year of occurrence. The p-values for each covariate indicate if the number of reported damages that occurred between March 9th and May 18th (corresponding to 2020 lockdown in Italy) differed between 2020 and the previous years (2016-2019).

	Damage type						
Year	**Livestock**	**Orchard**	**Poultry**	**Garbage**	**Building**	**Beehive**	**No. bears**
2016	0.372	-	0.396	-	-	0.765	**0.001**
2017	0.220	0.657	**-**	**<0.001**	**<0.001**	**<0.001**	**0.020**
2018	0.796	-	**0.022**	**-**	**<0.001**	**<0.001**	0.062
2019	0.469	0.341	**0.039**	**0.001**	**0.003**	**<0.001**	0.688

Table 2 - Results of the fitted Generalized Linear Models to assess brown bear proximity to hot spots for road network crossing, at different density of crossings, between 2019 and 2020, in the period March 9th - May 18th. Only the most parsimonious models are reported, based on model comparison via analysis of variance (ANOVA) and second-order Akaike Information Criterion (AICc) (further information in Table S5 and Table S6). For each covariate, the estimated coefficient values (b), the 90% confidence interval, and the P-values scores (*p <0.05; **p <0.01; ***p<0.001) are reported.

	Model 1	Model 2	Model 3	Model 4
Year(2020)	1.33 *** (0.91, 1.74)		2.48 *** (1.64, 3.33)	
Distance to all crossings	-0.59 *** (-0.79, -0.39)			
Distance to low density of crossings		-1.13 *** (-1.58, -0.68)		
Distance to medium density of crossings			-2.40 *** (-2.99, -1.80)	
Distance to high density of crossings				-2.24 *** (-3.03, -1.45)
Constant	-3.64 *** (-4.02, -3.27)	-4.54 *** (-5.04, -4.04)	-6.38 *** (-7.33, -5.44)	-5.73 *** (-6.67, -4.79)

Note: *p <0.05; **p <0.01; ***p<0.001

4. Discussion

It has been previously demonstrated that bears avoid anthropogenic disturbance over the landscape, particularly human mobility (Tattoni et al., 2015; Corradini et al., 2021). Interestingly, in this paper, we show that during the recent COVID-19 lockdown, bears responded by using spaces previously rarely used, although of high value for access to resources, or quality habitats. Our findings support the hypothesis that some species may respond to human presence and active disturbance, rather than infrastructure barriers per se (Corradini et al. 2021). Hence, brown bears likely considered humans as a major competitor temporarily removed from the landscape (Bates et al., 2020; Bates et al., 2021).

4.1 Temporal removal of human mobility

Between March 9th and May 18th 2020, bears have entered human-dominated spaces significantly more often compared to the same period of the previous years, as indicated by the increased occurrence of complaints (Figure 1). Importantly, because the number of such events was linearly rescaled based on bear abundance, with no significant variation in Trentino in the last two years (Table 1; Figure S3), our findings suggest that this pattern is unrelated to bear abundance. While these complaints should not be considered unusual *per se*, particularly given the large range of behavioural variations that bears can exhibit (i.e., “personality”; Hertel et al., 2020), the frequency of such events was unprecedented (Figure 1). During the period of the year considered, bears are biologically at a critical stage , with activity rising (i.e. post-den emergence, Figure S4), but habitat resources in the landscape still relatively scarce (Humphries et al., 2003). With no sensory stimulation associated with human activity (Halfwerk and Slabbekoorn, 2015), bears emerged from hibernation to find undisturbed spaces and availability of otherwise little accessible resources, prompting them to take advantage of these unexpected opportunities.

Complaints were spatially widespread in the region (Figure 2), indicating that at least a few individuals approached human-dominated areas during the lockdown. Bears' average behavioral expression can vary widely between individuals (Hertel et al., 2020), yet few, bolder individuals might have been responsible for the majority of the reported complaints in some years (Groff et al., 2020). Despite being more prone to cause conflicts, bold bears should not be considered 'unusual' animals, rather part of the population behavioral variation and critical individuals for its expansion in a human-dominated landscape (Lamb et al., 2020).

4.2 Disentangling human mobility and human infrastructure effects on animal movement

When lockdown measures due to COVID-19 pandemic were being enforced, brown bears demonstrated to approach hot spots linking high-quality areas (Peters et al., 2015) more, suggesting that connectivity temporarily increased as human presence decreased. This, together with the sharp increase of reported bear-related damages regarding settlement areas (e.g. poultry and garbage) or features normally protected by people (e.g. beehive and mountain buildings; Table S1), provides further evidence that space use and movement of bears are highly affected by 'functional anthropogenic disturbance' and not by human infrastructure *per se* (Corradini et al., 2021; Nickel et al., 2020). Bears have adapted to survive in an anthropic matrix relying on suitable habitat patches through niche partitioning (Martin et al., 2010; Lamb et al., 2020). In absence of their major competitor (i.e. human 'super predator', Smith et al., 2017) bears rapidly adjusted their space use by more evenly occupying the landscape, in accordance with the species' plasticity.

We demonstrated, using bear occurrence reports as ground-truth observations (Figure 2), that hot spots for road network crossings predicted by the connectivity model for Trentino brown bear (Peters et al., 2015) corresponded to actual bear use, especially when humans were absent. Additionally, during lockdown bears also used hot spots in otherwise underutilized portions of the suitable range, beyond the population core area (Figure 4). We argue that this temporary expansion indicates active human disturbance as a potential cause for the lack of a functional metapopulation after bear reintroduction. The use of hot spots of connectivity to reach the Eastern portion of Trentino (Figure 2), in particular, is promising towards the establishment of an Alpine-Dinaric metapopulation (Kaczensky et al., 2012), posited human disturbance decreases.

While human presence and activities have long been a part of the Alpine landscape, long-term coexistence with brown bears may only be achieved by reducing conflicts and human-caused mortality (Chapron and López-Bao, 2016; Lamb et al., 2020), while improving connectivity to facilitate the movement of animals in the landscape. In light of our findings, we suggest that restricting human mobility along predefined bear hot spots for road network crossing (e.g., reducing speed limits), or favouring alternative, undisturbed links (e.g., wildlife overpasses) could be effective ways to restore or improve connectivity.This should be paralleled by specific measures to reduce conflict, such as the protection of human property (i.e., beehives, poultry, or buildings), or anthropogenic food (i.e., bear-proof garbage bins) in future areas of expansions.

Understanding and quantifying the drivers that prevent animal metapopulations to be effective is essential for long term conservation and for the development of effective policies. We emphasize the importance of considering multiple types of human disturbance (sensu Nickel et al., 2020; Corradini et al., 2021) when predicting connectivity for animals on the landscape, particularly expanding large carnivores and other species that are subject to human competition or predation. While COVID-19 lockdown was a traumatic experience linked to a tragedy, our findings suggest that small-scale, pulsing modifications of human activity might be sufficient to notably increase bear connectivity, thus providing an encouraging example. In conclusion, we urge researchers and conservation planners to consider the non-negligible impact of human mobility on animal movement and connectivity in future studies.

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Declaration of Competing Interest

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: