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Ecological connectivity in the Alpine anthropic matrix

Natural reserves and corridors for the conservation of brown bear in the Alps (ABC - AlpBearConnect)

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Ecological connectivity in the Alpine anthropic matrix: Natural reserves and corridors for the conservation of brown bear in the Alps (ABC - AlpBearConnect)

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Grizzly bear in Grand Teton National Park, Teton County, Wyoming, USA. 2020. Picture by Andrea Corradini.

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Abstract

Large carnivores are among the most challenging species to conserve in our modern and crowded world. Having large spatial requirements and living in low density, they generally require wide and relatively undisturbed areas. In Europe, one of the most anthropized areas of the planet, these needs must be fulfilled in a complex human-dominated landscape. The reintroduced brown bear population living in the Central Alps represents one of the most emblematic examples of a constrained carnivore: despite a steady population increase in the first few years after reintroduction, the population did not substantially expand its range, nor has the Alpine-Dinaric metapopulation been reestablished as envisioned.

Although humans have lived in the Alps for centuries, little is known about their impact on the bear population. In other environments humans are known to function as a "super-predator" by changing habitats, competing for space, consuming resources, and harvesting, which alters the ecological niche of animals, especially large carnivores. This dissertation aims to evaluate this phenomenon by assessing the effects of human disturbance on brown bears in the Alps.

Anthropogenic disturbance is generally assessed by structural proxies, such as infrastructure and land use, which overlook the impact of human presence. In the first Chapter, we developed the Cumulative Outdoor activity Index (COI) to derive anthropogenic disturbance using crowdsourced data by Strava and validated it with ground truth observations derived from a local camera trapping survey. The intensity of COI provided an effective measure of functional anthropogenic disturbance, and it outperformed all commonly-used proxies of structural disturbance in predicting bear habitat use.

When displacement is not an option because of habitat limitations and social mechanisms, bear mobility may clash with human activity. During the moments of lowest mobility, such as resting periods, animals have decreased ability to cope with risky situations, and therefore the selection of suitable resting areas is crucial for the long-term survival of individuals. In the second Chapter, we measured multi-scale response to risk perception (i.e., COI) and resource proximity using bedding sites by GPS radio-collared adult brown bears in the Alps. To map resources across the study area, we developed a GIS-database combining spatial and non-spatial ecological information to map fruit availability. We observed that bears apply a security-food trade-off strategy, avoiding functional anthropogenic disturbance while in proximity to resources.

In the third Chapter, we explicitly tested the effect of an abrupt interruption of human mobility during COVID-19 lockdown on bears' use of ecological corridors. Using bear

occurrences reported to local authorities during the recent COVID-19 outbreak, we observed that bears used human-dominated areas more frequently, approached more intensively hot spots for road crossing network, and used areas further from the population core areas more often than previous years, suggesting that connectivity increased with reduced human mobility.

In a comparatively human-free system, for the fourth Chapter we used longitudinal morphometric data to analyze drivers of changes in body mass as part of an international collaboration with biologists studying the grizzly bear in the Greater Yellowstone Ecosystem. Specifically, we analyzed changes in lean body mass and fat percentage during years of major ecosystem perturbations. We observed that individual lean body mass during the last two decades was primarily associated with population density, but not body fat percentage, showing density-dependent factors.

Our combined findings (Chapters 1-3) showed that brown bears have to adapt their space use, movement, and resource proximity as a result of functional anthropogenic disturbance. In Chapter 4 we explored one effect of unconstrained bear space use on individuals, as manifested through density-dependent effects on body size. In the Alps, however, we found multiple instances of the human-super predator outcompeting bears so as to make density-dependent effects likely less significant as compared to human-caused mortality. These effects could occur in a variety of socio-ecological contexts across Europe, jeopardizing the long-term establishment of both newly reintroduced bear populations, as well as spatially limiting those naturally present in the environment. In response to disturbance, bears have had to reduce their ecological niche in human-dominated landscapes. Allowing humans and bears to coexist in the same landscape is a challenging task, but it is essential for the long-term survival of this newly reintroduced population that are otherwise at risk of extinction.

Introduction

Large carnivore conservation in the Anthropocene

Human influence on the Earth's ecosystem has now reached the scale and intensity of some of nature's most powerful forces (Steffen et al., 2011). With the arrival of Europeans in the Caribbean in 1492, and with the great technological advancement of the following centuries (i.e., initiated with the Industrial Revolution, approx. 1760), humans have had such a dramatic impact on the Earth that they have caused significant changes to terrestrial and marine ecosystems as a result of their use (Lewis and Maslin, 2015). These changes will be detectable in the geological stratigraphic record for millions of years, prompting scientists to coin the term "Anthropocene" to refer to a geological epoch dominated by humans (Crutzen and Stoermer, 2000; Crutzen, 2002). The consequences of the human footprint on the Earth's ecosystems are numerous, ranging from global-level perturbations such as climate change (Solomon et al., 2009) and land-use shifts (i.e., habitat loss, degradation, and fragmentation) (Hoekstra et al., 2005) to more localized changes in species community occupancy (Wang et al., 2015; Boron et al., 2019) and animal movement and behavior (Tucker et al., 2018). Many species have already been lost as a result of recent anthropogenic disruptions (defined as the “sixth mass extinction”), and many more are in danger due to small geographic ranges and low population abundance (Barnosky et al., 2011). Given their ecological requirements, large-bodied animals are particularly susceptible to human disturbance and competition among vulnerable species (Cardillo et al., 2005), which puts them at risk if the current scenario of human expansion and land-use change is not halted or reversed.

Large carnivores, the large-bodied members of order Carnivora, are considered among the most challenging species to conserve in our modern and crowded world (Chapron et al., 2014; Ripple et al. 2014). They require wide, relatively undisturbed areas because of their large spatial and habitat requirements, low population density, and slow life histories. They also require a diverse, abundant, and stable prey (or plant) biomass due to their high energy requirement (Carbone et al. 1999; Boitani & Powell, 2012). Because of their ecological niche, large predators play a key role in the Earth's environments, exerting strong regulatory effects on many ecosystems (i.e., through top-down mechanism; Suraci et al. 2019) and thereby improving the resilience of the ecosystems in which they thrive, both directly and indirectly (Ripple et al., 2014). Despite their significant ecological role, most large carnivore species are of conservation concern, and major coexistence issues remain unsolved globally, mostly because of conflicts with humans, livestock, and game species

(Ripple et al., 2014). Recently, two alternate scenarios for coexistence between humans and large carnivores in the contemporary world have been proposed: (i) the “separation model”, where people and predators are kept apart, with large carnivores persisting in inaccessible (i.e., fenced) or remote wilderness areas, and (ii) the “coexistence model”, where people and predators are allowed to share the landscape (Chapron et al., 2014). The first scenario has long been seen to be the most straightforward to implement, owing to the virtual lack of human-predator conflicts (“land-sparing”). However, the latter scenario (“land-sharing”) has recently emerged, aided by both the recovery of some large carnivore species and the global expansion of human influence, requiring carnivores to coexist in anthropogenic landscapes (Chapron et al., 2014; Lamb et al., 2020).

In Europe, one of the most anthropized areas of the planet, the persistence of large carnivores must be assured in a complex human-dominated landscape (i.e., “coexistence model”) (Chapron et al., 2014). Primeval habitats are now rare in the continent and significant human influence on the composition, structure, and functionality of ecosystems has persisted for millennia. Particularly, recent decades were marked by social, structural, and ecosystem transformations, which transformed Europe's cultural, economic, and ecological landscape. Increased habitat availability and lower human population density, as well as favorable human tolerance and policy, have favored the expansion of large carnivores in particular (Cimatti, et al., 2021). In the Alpine region, such landscape and cultural changes have been paramount. Traditional pastoral activities and agriculture on less productive and accessible terrain were abandoned in the last decades (Laiolo et al., 2004; Tasser et al., 2005; Tattoni et al., 2017), but on the other hand, farming and human land use are being intensified in the major valleys (Tasser et al., 2005), while outdoor recreation activity has expanded throughout the Alps (Schirpke et al., 2018). Territories abandoned by humans have reverted to natural habitats and served as connecting bridges for re-establishing carnivore species, while greater competition for space and decreased landscape connectivity have emerged in regions with significant human development. Large carnivore populations have partially recovered in the last 20 years (Boitani, 2018; Huber, 2018; von Arx, 2020), and given the scarcity of wilderness areas in comparison to African and North American landscapes, the recovery is opening up new research opportunities, especially as the “land-sharing” scenario becomes more prevalent in the Alpine environment and across Europe (Chapron et al., 2014).

By sharp contrast, human activities are minimal in ‘true' wilderness areas found in certain areas of the world, where large carnivores can carry out their spatial and ecological requirements without the need of competing with humans (Chapron et al., 2014). The

Greater Yellowstone Ecosystem, one of the world's largest and best-preserved temperate ecosystems, is one of the best examples of wilderness. The ecosystem encompasses the Yellowstone National Park, a ~9,000 km^2 wildlife sanctuary and the world's first National Park, as well as vast federal lands where human presence and activities are regulated. Seven large predators thrive in the ecosystem, and despite the influence of human land use (particularly outside the National Park), large carnivores and humans are largely separated (Chapron et al., 2014). Because of its characteristics, this ecosystem provides a unique opportunity to study the behavior, movement, habitat use, and life-history traits of animals living in a relatively human-free environment. Large carnivores in Yellowstone National Park have been the subject of pioneering wildlife research, including radio telemetry and wildlife tracking. From the early 1960s, the Craighead brothers used radio tracking systems and satellite monitoring to study the movement of grizzly bears (Craighead et al., 1963) or to retrieve environmental and physiological data from a hibernating black bear (Craighead et al., 1971). These studies laid the groundwork for modern telemetry, which has evolved into one of the main tools for ecologists studying wild animals in their natural habitat (Cagnacci et al., 2010). In addition, the reintroduction of gray wolves into Yellowstone National Park in the mid-1990s was arguably one of the most significant wildlife conservation efforts of the twentieth century (Bangs and Fritts, 1996), both symbolically and environmentally (Smith et al., 2003), and it sparked research on trophic cascades in large mammal communities (Ripple and Beschta, 2012). With the current worldwide upheavals brought about by humans, the Greater Yellowstone Ecosystem is more relevant than ever for ecological research on animals, but in particular large carnivores.

Resource selection, movement, and landscape connectivity in an anthropic matrix

A pivotal concept in ecology is the scale at which ecological phenomena should be studied (Levin, 1998). Systems show different variability on a range of organizational scales (Mayor et al., 2009), and the decision of the scale at which to study the system is crucial. In habitat selection studies, for example, behavioural scales (Johnson, 1980) based on observations of individual distribution or movement are widely used. The observational scale can be arbitrarily chosen depending on the research objective (Levin, 1998; Mayor et al., 2009), however to minimize the perceptual bias with which a system is observed and studied, different scales might be investigated (Ciarniello et al., 2007), or incorporated (DeCesare, et al., 2012) in an attempt to reconcile scale dependence when finding patterns of selection and avoidance. Human disturbance, for example, can influence the selection of habitats and resources in large carnivores (Ciarniello et al., 2007; Sánchez et al., 2013; Zimmermann et al., 2014), and animals in general (Peters and Otis, 2007; Plante et al., 2020), at different spatial and temporal scales. Understanding these scale-dependent drivers of selection can help synthesizing patterns within, and across, populations (Mayor et al., 2009). To this purpose, a multi-scale analysis of the impact of anthropogenic disturbance (i.e., "coexistence model"; Chapron et al., 2014) may aid in determining the driver of individual and population-level selection, as well as the impact of such disturbance on niche formation, and ultimately fitness.

Despite the necessity of investigating disturbance at multiple ecological scales, it is important to emphasize on drivers of large-scale selection and avoidance, notably mobility, in large-bodied mammals. Due to their energetic constraints, large carnivores (i.e., species with body masses larger than 21.5 kg; Carbone et al., 1999), must travel great distances and maintain large home ranges in order to locate mobile prey or other adequate food sources, compensating for energy conversion loss through the food web. Therefore, unconstrained movement and connectivity in the landscape are crucial to allow large carnivores to carry out their ecological functions, such as trophic interactions, dispersing, mating, or even disperse seeds (Boitani & Powell, 2012; Ripple et al., 2014; García-Rodríguez et al., 2021), over large spaces. Furthermore, maintaining immigration and emigration across breeding subpopulations at the metapopulation level, particularly for recovering isolated populations, prevents inbreeding, genetic drift, demographic decline, and, in extreme circumstances, extinction (Elmhagen and Angerbjörn, 2001). The free movement of animals is particularly important in those landscapes where people and predators share the space (Chapron et al., 2014). Despite emerging scenarios in which carnivores exist in human-dominated landscapes (Chapron et al., 2014; Lamb et al., 2020), recent research has demonstrated that animal movement, including large mammals, is constrained or altered as a result of human footprint around the world (Tucker et al., 2018). In continental Europe, the re-establishment of large carnivore populations has clashed against major threats, such as geographic (i.e., major roads and human settlements) and functional (i.e., human mobility, social acceptance, or socioeconomic factors) barriers. With the rapid development of the infrastructure network over the last few decades, there has been a significant amount of research on the impact of geographic barriers on animals, also prompted by the need to reduce wildlife-vehicle collisions (i.e., road ecology; Forman et al., 2003; Fahrig and Rytwinski, 2009). Functional barriers, on the other hand, have just recently been recognized as severe threats to landscape connectivity. The development of indicators of human presence (Nickel et al., 2020;

Goodbody et al., 2021) and tolerance (Behr et al., 2017; Struebig et al., 2018) toward large carnivores has only recently gained interest, yet "anthropogenic resistance" in connectivity evaluation has been rarely implemented (Ghoddousi et al., 2021), particularly with respect to human mobility. Understanding the full extent of landscape connectivity in an anthropic matrix, net of both geographical barriers and "anthropogenic resistance", would enable researchers, conservationists, and managers to develop increasingly realistic scenarios of "effective connectivity" (Robertson et al., 2018; Van Moorter et al., 2021) for large carnivores.

The brown bear *Ursus arctos*

Among terrestrial large carnivores, the brown bear is one of the largest and most widely distributed members of the order Carnivora. In the Holarctic region, approximately 110,000 mature individuals are distributed among 44 subpopulations, some of which are of conservation concern (McLellan et al., 2017). Their widespread distribution is a result of their capacity to thrive in a variety of environments and to consume a range of food sources, as well as their large home ranges and solitary social structure (McLellan et al., 2017). Ecologically, brown bears are important ecosystem engineers, playing a critical role in the Earth's environments with their niche construction behavior, such as increasing soil elements (Tardiff & Stanford, 1998), create microhabitat (Miller, 1990), act as seed dispersers (García-Rodríguez et al., 2021), or exert a regulatory effect in the food webs (i.e., as omnivores; Kratina et al., 2012). Due to their ecology, longevity, ability to track resources without being territorially bound, and reduced natural competition (aside from conspecifics), brown bears represent a good case study for looking at the effects of anthropogenic disturbance on large carnivores. Indeed, bears that share the landscape with humans face significant challenges and must adjust to the presence of the human "super-predator" (Smith et al., 2017) despite their distinct ecological adaptability. Historically, this coexistence has resulted in bear population isolation or even extinction in some regions (Mattson et al., 2002; Chapron et al., 2014), while more recently, anthropogenic disturbance has been reported to alter the habitat use (Martin et al., 2010), diet (Kavčič et al., 2015), circadian rhythms (Ordiz et al., 2017), and life-history traits (Bischof et al., 2017) of bears. Space is a particularly scarce resource in human-dominated environments; as a result, many aspects of bear ecology that are dependent on space availability, such as resource acquisition, movement, and landscape connectivity, are compromised. In an ever-changing world, understanding the multi-scale anthropogenic effects on brown bears will be critical for guaranteeing their long-term coexistence in human-dominated landscapes (i.e., as in an ecological community; Chapron and López-Bao, 2016), but also ensuring the functionality of terrestrial ecosystems.

Aims and objectives

The aim of this research was to determine the ecological scales at which various forms of anthropogenic disturbance have an effect on space use, niche construction, movement, and ultimately connectivity in the reintroduced brown bear population living in alongside humans (i.e., "coexistence model"; Chapron et al., 2014). Additionally, as a comparison, we aimed to determine the density-dependent factors, while controlling for density-independent factors, affecting individual performance in grizzly bears living in a relatively human-free landscape (i.e., "separation model"; Chapron et al., 2014). In particular, the main objectives of this Ph.D thesis were: (i) to assess the effect of different types of anthropogenic disturbance on a reintroduced brown bear population living alongside humans; (ii) to understand the ecological scale at which human-induced disturbance affects the niche formation of individual brown bears; (iii) to determine the effects of human activity when predicting connectivity for bears on the landscape; (iv) to investigate the demographic determinants in a brown bear population that lives in a largely human-free environment. Objectives (i), (ii), and (iii) were investigated using telemetry and individual data collected from the brown bear population in Trentino/Central Alps (Huber, 2018), while objective (iv) was investigated using longitudinal data collected from the grizzly bear population in the Greater Yellowstone Ecosystem. The Alpine bear population, along with the Pyrenean bear population, is one of the two reintroduced populations still extant on the European continent (Huber, 2018). Brown bears are protected continent-wide under European legislation (Habitats Directive 92/43/EEC), except for the removal of selected individuals under derogation of Article 16(1) (Epstein et al., 2018). Yellowstone brown bears, often known as grizzly bears, can be found in the Greater Yellowstone Ecosystem, which spans part of Idaho, Montana, and Wyoming. Grizzly bears in the contiguous continental United States are currently protected under the Endangered Species Act of 1973 (16 U.S.C. 1531), and individuals can only be relocated or removed only if it is deemed absolutely necessary.

The thesis is organized into four chapters with the main goal of examining the overall effects of anthropogenic disturbance on two brown bear populations on opposite ends of the human disturbance spectrum. In Chapter I, we decoupled the effect of different types of anthropogenic disturbances in predicting bear habitat use at the home range level. We did so by developing the Cumulative Outdoor Activity Index (COI), which uses human mobility data to estimate anthropogenic disturbance, and comparing it to commonly used structural disturbance proxies (i.e., infrastructure and human settlements). In Chapter II, we measured multi-scale response to risk perception (i.e., based on human mobility; COI) and food resource proximity by examining the brown bear selection of home ranges and bed sites locations. For tracking food resources in the landscape, we developed a GIS-database incorporating spatial and non-spatial ecological information to map fruit availability across the study area. In Chapter III, we examined the effectiveness of previously predicted ecological corridors for the Alpine bear population by testing the effect of a sudden reduction of human mobility bear use of ecological corridors. For this purpose, we used spatially explicit bear-related complaints filed to local authorities during the recent COVID-19 lockdown (9 March to18 May 2020) in Northern Italy. In Chapter IV, we looked at the primary factors that influence individual growth and performance in grizzly bears in an environment with relatively low anthropogenic disturbance. Using longitudinal morphometric data spanning more than 40 years, we assessed the density-dependent drivers of changes in body composition over time, while accounting for external environmental factors such as management practices and food resource fluctuations.

Individual-based relational spatial database

In the province of Trento, brown bears have been continually monitored and genetically sampled by various authorities since the reintroduction project in the early 2000s. This long-term monitoring, combined with technological advancements and the desire to minimize data significance loss through time, has prompted the development of a comprehensive and scientifically valuable dataset. As a result, an individual-based spatial relational database has been implemented, pooling a large amount of multi-source georeferenced data available in the Central Alps. The database is the product of years of expertise gained through the EURODEER network (https://eurodeer.org/), which is now a part of the wider EUROMAMMALS project (http://euromammals.org/). The spatial database was implemented using PostgreSQL (PostgreSQL Global Development Group, 2016) with the PostGIS extension, thus taking full advantage of the software's features, including data integrity, data consistency, storage capacity, reduced data redundancy, long-term storage, and advanced authorization policy (allowing the sharing with partner institutions) (Urbano and Cagnacci, 2014). Additionally, PostgreSQL's high level of interoperability enabled the development of a seamless workflow with data analysis software, such as R, (R Core Team, 2020) and GIS applications, such as GRASS (GRASS Development Team, 2018) and QGIS

(QGIS Development Team, 2019). The spatial database, to date, contains GPS location data (n≈ 80,000 fixes) and activity data (n≈ 1,700,000) from sensors deployed on 18 bears, as well as genetics, kinship, damages, VHF radio tracking, sightings, and tracks information (n≈ 9.000 records) for 152 bears (including the individuals equipped with GPS collars). The complete database structure, as well as the SQL code used to generate the data repository, is freely available on GitHub (https://github.com/feurbano/bear_data).

Grizzly bears have been monitored in the Greater Yellowstone Ecosystem by the Interagency Grizzly Bear Study Team (IGBST) since 1973. The IGBST is an interdisciplinary group of scientists and biologists formed by the Department of the Interior, with members from the U.S. Geological Survey and various Federal, State, and local bureaus (van Manen et al., 2020). Since 1975, the IGBST has radio marked 973 individual grizzly bears in the whole Greater Yellowstone Ecosystem, along with a large set of ancillary data such as genetics, activity data, kinship, mortality, and morphometrics (van Manen et al., 2020), making it one of the world's best-monitored bear populations. The database is primarily utilized to meet the IGBST's objectives, which include long-term monitoring of the grizzly bear population in the GYE, as well as the study of bear habitat use and the relationship between land management operations and bear population welfare. Nonetheless, the 50 years long dataset has resulted in a plethora of technical and scientific publications that contributed significantly to our understanding of brown bears worldwide.

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Chapter 1

Effects of cumulated outdoor activity on wildlife habitat use

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Abstract

Humans profoundly affect animal distributions by directly competing for space, not only transforming, but actively using their habitat. Anthropogenic disturbance is usually measured via structural proxies such as infrastructure and land use that overlook the impact of human presence, or functional disturbance. In this study, we propose a methodology unifying two paradigms, human mobility and animal movement, to fill this gap. We developed a novel spatially-explicit index of anthropic disturbance, the Cumulative Outdoor activity Index (COI), and validated it with ground truth observations derived from camera trapping ($r = +0.63$, $p < 0.001$). Building on previous work from Peters et al. (2015, Biol. Cons. 186, 123–133) on a Critically Endangered brown bear population in the Alps, we used Resource Selection Analysis to assess the influence of different forms of anthropogenic disturbance on the relative probability of habitat selection. The intensity of COI provided an effective measure of functional anthropogenic disturbance, and it outperformed all alternative and commonly-used proxies of structural disturbance in predicting bear habitat use. Our predictions suggest that brown bear shrinks its ecological niche as a consequence of intense human use of otherwise suitable habitat. These constraints may limit the potential range expansion of bears to establish a viable Alpine-Dinaric metapopulation. Conclusive conservation and future land use planning towards human-wildlife coexistence should account for the functional presence of humans on the landscape. The proposed COI could help determine where mitigation measures should be enforced.

Keywords: Strava; COI; Bio-logging; Human-wildlife conflict; *Ursus arctos*; Habitat selection.

Introduction

Human impact has become the most relevant determinant of animal species distribution and persistence, with the extirpation of populations and extinction of species occurring at an unprecedented rate (Ceballos et al., 2015). Alongside indirect modification of abiotic conditions (i.e., pollution, climate change) (Pecl et al., 2017), harvesting (Ripple et al., 2016), and the introduction of invasive species (Gallardo et al., 2016), humans affect animal distribution by directly competing for space. Several methods have been applied to assess the effect of habitat fragmentation, urbanization and connectivity loss on animal population distribution, occurrence, and space use behavior (Compton et al., 2007; Crooks et al., 2011; Panzacchi et al., 2016; Prokopenko et al., 2017). Recently, by using the Global Human Footprint Index, Tucker et al. (2018) showed that mammal species moved shorter distances under high human exposure. These analyses mainly utilized structural (i.e. passive) proxies of human competition for space based on infrastructure, land use, human accessibility (e.g., linear features such as roads, land- and waterways), and encroachment (e.g., population density, nightlights). However, direct competition for space should emerge by functional (i.e. active) utilization of the aforementioned infrastructures, specifically human mobility.

Human mobility has exponentially grown in the Western world after WWII (Freund and Martin, 1993), and globally in the last 3 decades (Susilo et al., 2007). An entire branch of human geography is dedicated to the measurement and analysis of human mobility (Barbosa et al., 2018) and has been spurred by the global spread of personal tracking devices (e.g., navigation systems, mobile phones, GPS watches). Human mobility big data are analyzed for many applications, from marketing (Wedel and Kannan, 2016), to traffic control (Herrera et al., 2010), and rescue services (Amin et al., 2012), which target human behavior and space use. Only a few studies can be found that assess the impact of human mobility on wildlife, with the exception of a wide literature on traffic and roadkills (Trombulak and Frissell, 2000; Coffin, 2007; Dean et al., 2019). Beyond motorized mobility, human presence in wild habitats at the fine scale has been assessed using camera traps (Oberosler et al., 2017) or handheld tracking devices (Moen et al., 2012; Squires et al., 2019).

Recently, a diversity of mobile device software applications to track recreational outdoor activities, such as hiking, running or cycling, have become increasingly popular. In particular, the tools provided by Strava (San Francisco, CA, USA) are used worldwide to track user movements and access a crowdsourced Global Heatmap (Strava, 2018a). The Global Heatmap is a visualization of the cumulative outdoor activity tracks recorded and marked as public by users, with monthly updates. Since its establishment as a tracking app, trajectories have been uploaded at an exponential rate, reaching over two billion records (Strava Press, 2018a), making the Global Heatmap the world's largest freely-viewable collection of GPS-tracked human outdoor activities of its kind. Strava data (Strava, 2018b) have been used for urban planning purposes or public health studies (Table S1.1). Despite this great potential, Strava-derived data have never been integrated into ecological studies.

In this work we introduce the Cumulative Outdoor activity Index (COI), a novel spatially-explicit index of anthropic disturbance based on the Strava heatmap, and used to assess active competition for space as opposed to structural indicators of anthropic disturbance (i.e., human settlements and linear features such as trails or roads). Building on previous work from Peters et al. (2015), we modeled habitat selection by a brown bear population reintroduced in the Eastern Italian Alps (Fig. 1) as a critical case study. Brown bears were reintroduced in Western Trentino in the early 2000, after the local population had been functionally extirpated, with the goal to reestablish a Alpine-Dinaric metapopulation (Duprè et al., 2000; Kaczensky et al., 2012). Despite the steady population increase in the first period after reintroduction, it did not substantially expand its range, nor was the goal to reestablish an Alpine-Dinaric metapopulation met. As a result, the Alpine brown bear population remained isolated and was listed as Critically Endangered due to the low number of mature individuals (< 50, Criteria D1; IUCN, 2001) (Huber, 2018). Conversely, human-bear conflict emerged (Groff et al., 2019) and several bears died from anthropogenic causes (Tenan et al., 2016). We hypothesize that direct competition for space with humans has limited the selection of preferred sites within the home ranges of bears, more so than environmental restrictions and structural proxies identified in previous studies (Duprè et al., 2000; Peters et al., 2015). Given that biological processes can be observed and interpreted differently at various scales (Ciarniello et al., 2007; Mateo Sanchez et al., 2014), we considered the relative effect of anthropogenic disturbance at the home range scale (i.e., third-order selection; Johnson, 1980).

Materials and methods

Assessing functional anthropic disturbance: the Cumulative Outdoor activity Index

In order to assess the active competition for space between humans and wildlife, we developed an index measuring the effective use of structural linear features, or any portion of the habitat, through outdoor activities. For this purpose, we visualized and processed the

Strava Global Heatmap (Strava, 2018a) at the highest resolution freely viewable online without registration (i.e. 20 m, or zoom level 13 OpenStreetMap Wiki contributors, 2019).

Strava Global Heatmap structure

The Strava Global Heatmap displays a color gradient of outdoor activity tracks (rides, runs, water, and winter activities) recorded by users, where brighter tones (i.e., higher heat) represent an intense use, i.e. many overlapped activity tracks. Activity tracks are recorded as ‘pixel paths’ connecting consecutive GPS locations (Robb, 2017), so that the count of paths overlapping in each pixel corresponds to a raw ‘heat’ count. Such counts are then normalized to the bounded range (0,1) using a Cumulative Distribution Function (CDF), and weighted with respect to the neighbor context of intensity of use (i.e., the heat values are not comparable at a large distance, but are comparable in the proximity- about 50 km diameter at our zoom level, see below). For more technical details on how the Strava Global Heatmap is built, see Supporting information S2.

Deriving the Cumulative Outdoor activity Index

We derived the Cumulated Outdoor activity Index using the freely viewable Strava Global Heatmap. The approach requires few parameters and it is best achieved in a GIS environment. The extraction took place as follows: (i) an area of interest (Western portion of Trento Province, Fig. 1, and paragraph ‘Study area’) was displayed in the Strava Global Heatmap website (Strava, 2018a); (ii) we set the zoom level to 13 (OpenStreetMap Wiki contributors, 2019), the highest displayable without the need to register with a private account; (iii) we set the Heatmap Colour as “blue” (see below), the desired Activity Type to “All”, the Heat Opacity to 100%, and we removed all background layers; (iv) we took a screenshot of the displayed area and saved it as a raster PNG image; (v) we georeferenced the raster image in a GIS environment using 6 control points. We used the WGS 84/Pseudo-Mercator Coordinate system (EPSG: 3857), as it was the projected coordinate system used to build the Global Heatmap (Robb, 2017); (vi) we repeated the procedure as many times as needed to cover the entire study area, and merged all the georeferenced raster layers; (vii) we manually removed the activities overlaying ski slopes and water bodies, which were not of interest for the purpose of this study, using subtracting masks obtained from local geographic layers (Autonomous Province of Trento, 2019); (viii) we displayed single pixels as a 256-element color spectrum array (Robb, 2017), so that when the aggregated activities are shown as “blue”, the array matches perfectly the Blue color spectrum of an RGB color model (0, 255); (ix) we rescaled the value so the index (COI) ranged from 0 to 1.

Validation of COI through ground truth observations

In order to validate the COI as an honest proxy of human use of wildlife habitats, we compared its values with human detections obtained via independent counts recorded on camera traps. In a subset of our study area (Fig. 1), an extensive, systematic camera trap survey (n = 60) was conducted (Oberosler et al., 2017; see Supporting information for details), recording both wildlife and human presence along forest roads and trails (30 sites in each category). Human passages were recorded either as pedestrians/bikers or vehicles (cars, motorbikes, tractors, and trucks). We considered the former as ground truth observations, and excluded the latter as not matching the purpose of this study. We tested the validity of the COI by comparing it with ground truth observations, measured by the number of 'independent' human events per site, i.e., sequential detection events separated by an interval of 1 h. First, we extracted the value of COI associated with each camera trapping site. To account for spatial imprecision, we drew a 50 m radius buffer around each trapping location and extracted the 95th percentile COI value within that buffer. We finally tested the statistical dependence between COI values and number of human detection events using Spearman's rank correlation coefficient (Spearman's ρ).

A case study: assessing the effect of anthropogenic disturbance on a reintroduced brown bear population

We applied our proxy for functional human disturbance, measured as cumulated outdoor activity, to evaluate habitat selection and predict probability of space use in a reintroduced population in Trentino, Central-Eastern Italian Alps. We used the same third-order Resource Selection Analysis (RSA) as Peters et al. (2015).

Study area and brown bear population

The study was carried out in the Province of Trento, a 6.200 km^2 (Fig. 1) area characterized by rugged mountainous terrain (from 65 to 3769 m a.s.l.) and covered by forests and prairies according to the altitudinal succession. Valleys are largely human-dominated (87 inhabitants/km^2), with a developed network of roads and railways (density = 95 km/100 km^2). The vast infrastructural system of the Adige basin effectively constitutes a connectivity barrier for many animal species, dividing the study areas into two sectors (Fig. 1). Between 1999 and 2002, 10 adult bears from Slovenia were released in the Adamello Brenta Nature Park, Italy (PACOBACE, 2010). The newly established population colonized large parts of Western Trentino. In the study period, the brown bear population estimates (2012–2018) varied from 29 to 55, as a result of a positive, albeit variable, growth rate since 2002 (Groff et al., 2019). However, the population is still listed as Critically Endangered due to the small number of mature individuals (<50, Criteria D1; IUCN, 2001) (Huber, 2018). The brown bear is currently protected under European (Habitats Directive 92/43/EEC) and Italian Laws (L. 157/92), except for the removal of bears considered as dangerous (PACOBACE, 2010).

Movement data

We used the GPS trajectories of animals collared between 2011 and 2019 (8 females, 4 males; Vectronic GPS–GSM collars, Vectronic Aerospace GmbH, Berlin, Germany) for a total of 21 animal/year as part of monitoring activities undertaken by the Autonomous Province of Trento (PACOBACE, 2010; Supporting information for further information on trapping and handling). The number of surveyed individuals corresponded to about 25% of the estimated yearly average of bears in the study period (about 45 bears/year; Groff et al., 2019). The trajectories were limited to non-hibernating periods and regularized at a 6-hour fix rate using the functions in the R package adehabitatLT (Calenge, 2006), excluding a-priori data collected with less frequent schedules.

Environmental layers

First we extracted core environmental covariates based on Peters et al. (2015), using newer spatial layers with higher resolution and accuracy where possible, including topographic variables (altitude, slope), canopy cover, and land use (cultivated lands without orchards). We used the distribution of human settlements and linear infrastructure (trails, unpaved forest roads, and main paved roads) as proxies for structural human disturbance, as well as a combined composite layer (Table S5.1). Finally, we used the newly-derived COI as a proxy of functional anthropogenic disturbance (Table 1). All raster layers were resampled to a spatial resolution of 20 m pixel size (see Supporting information S5) and were rescaled by min-max normalization to a defined range of 0 and 1.

To create the structural disturbance layers, we generated a raster proximity map based on Euclidean distance of each cell to the nearest infrastructure. We then transformed the maps to exponential decays in the form of

$$sd = 1 - e^{-\alpha d} \tag{1}$$

with sd = structural disturbance, $\alpha = 0.002$ and d = distance (m) to a given linear feature (Nielsen et al., 2009). This transformation drastically reduced the effect of linear features beyond a few hundred meters, making large distances essentially irrelevant (e.g. >1500 m). The resulting values for sd range from 0 (at $d = 0$) to 1 (for large values of d). Using Eq. (1), structural disturbance layers were calculated for Distance from Human settlements (DHS), Distance from Main Roads (DMR), Distance from Forest Roads (DFR), Distance from Human Trail (DHT), and Distance from Roads and Trails (DRT) (Table S5.1). Furthermore, for both structural and functional disturbance, we computed derived spatial covariates expressing the ‘density of disturbance’ (cumulated disturbance per spatial unit). Specifically, we summed COI and the values of the raster layer combining all linear infrastructure features (roads and trails), both ranging (0,1), within a 11 × 11 pixel moving window (dCOI, dRTN: Table S5.1). This accounts for the spatial context around each pixel and potentially for spatial perception of disturbance by bears (~100 m; Moen et al., 2012). We performed a correlation analysis (Hinkle et al., 2003; Fig. S5.1) between all variables, thereafter building a priori models to evaluate the respective contribution of human disturbance metrics to bear habitat selection, with covariates within the same model having $|r| \leq 0.6$ (Peters et al., 2015).

Resource Selection Analysis

We fit a Resource Selection Function (RSF) to estimate the probability of use by bears of given resource units (Manly et al., 2002). We applied a used/available design and estimated selection within individual home ranges, i.e. third-order selection scale (Johnson, 1980). We considered GPS fixes as used locations and calculated individual bear's annual home range by Kernel Density Estimation (Worton, 1989) using the R package adehabitatHR (Calenge, 2006). We calculated 90% fixed kernel home ranges using href as smoothing parameters (Worton, 1989). We sampled twice as many available than GPS-based used locations to have better parameter estimates while maintaining reasonable computational times (Northrup et al., 2013). We extracted all the environmental covariates described above at each of the used and available locations.

We evaluated how anthropogenic disturbance influences space use behavior of brown bears in Western Trentino by testing five alternative hypotheses, corresponding to a set of a-priori RSF models (“Models of Disturbance”, MD; Table 1). Specifically, a core environmental model with slope, TCD and CORINE land cover as predictors (to represent respectively topography, canopy cover and land use effects) was complemented by one or more variables describing different aspects of structural disturbance (DHS, DMR, DFR, DHT, DRT, dRTN; giving models MD1 to MD4, Table 1). Similarly, we complemented the core model with the index of functional anthropogenic disturbance dCOI (model MD5, Table 1). We thus fitted each RSF model using a Generalized Linear Mixed Model (GLMM) with a binomial error distribution via maximum likelihood, using a Laplace approximation. We included all the covariates as additive fixed terms and individuals as random intercept to account for autocorrelation (Gillies et al., 2006), as the purpose of this study was to quantify population-level variations as a response. We performed model selection using the Akaike Information Criterion (AIC).

We predicted the relative probability of use based on selection coefficients of the best fitting model for all pixels in the given area (Fig. 1) using the function *predict()* in the R package raster (Hijmans, 2017). Afterwards, we tested the predictive capability of the RSF model via 10-fold cross-validation (Boyce et al., 2002), measuring the performance of the spatially explicit predictions with the set of random training and test subsets using Spearman's rank correlation coefficient. We managed, processed, and analyzed the data entirely on the free and open-source software QGIS 3.4.4 (QGIS Development Team, 2019), GRASS 7.4 (GRASS Development Team, 2018), and R 3.4.3 (R Core Team, 2017) under Ubuntu 16.04.3 LTS (Canonical Ltd., London, United Kingdom). Results were reported in tables created with the R package stargazer (Hlavac, 2018).

Results

Validation of COI as an index of functional human disturbance

The camera trap survey yielded 1262 independent events of humans both as pedestrians/bikers over a period of 30 consecutive days across the 58 camera traps that functioned well. Of these events, 514 were recorded on trails and 748 on unpaved roads. The median count of people per camera was 21.76 (IQR 2.25 to 33.50, range 0 to 108), while the median of the extracted COI values per camera was 0.08 (IQR 0.00 to 0.39, range 0 to 0.71). We found a positive, statistically significant Pearson correlation between the Cumulated Outdoor activity Index and the number of human detection events ($r = +0.63$, $p < 0.001$; Fig. S6.1).

Anthropogenic disturbance effect on bear habitat selection

Within their home range (mean home range size = 259.51 km^2, with IQR 40.50 km^2 to 313.43 km^2; see Supporting information S7 for details), bears selected for steep areas and high canopy cover and strongly avoided areas with high density of functional disturbance according to the newly developed COI (most parsimonious model: MD5, Table 2; $b_{dCOI} = -5.048$, $p < 0.001$). Importantly, the effect size of dCOI was considerably larger than any other predictor in the candidate models. Still, most predictors indicating habitat disturbance showed a significant (and often strong) effect in less supported, alternative models. Bears avoided proximity to human settlements (MD1: $b_{DHS} = 2.584$, $p < 0.001$; $\Delta AIC = 97$ with respect to the best model; Table 2) and areas with high density of structural disturbance, parameterized in the models by the density of roads and trails (dRTN) (MD4: $b_{dRTN} = -2.587$, $p < 0.001$; $\Delta AIC = 328$ with respect to the best model; Table 2). When considering the influence of specific linear disturbance (MD3, ΔAIC = 362 with respect to the best model; Table 2), the bear showed quite different responses, avoiding areas in proximity to main roads ($b_{DMR} = 0.935$, $p < 0.001$), but selecting for human trails ($b_{DHT} = -0.198$, $p < 0.001$). Interestingly, bears did not seem to either avoid or select forest roads ($b_{DFR} = 0.057$, $p > 0.05$). The predictors of the core model maintained similar coefficients in all models (Table 2), with the exception of cultivated lands without orchards (AGR), not significant in some models and marginally significant in others (Table 2). However, the core model *per se* was the least supported by the data than all of Models of Disturbance but MD2 (Generic Linear Disturbance). The best fitting model (MD5; Table 2) led to robust spatial predictions of the relative probability of use by brown bear in the study area (Fig. 2; average Spearman's correlation coefficient for the 10-fold cross validation: $r = +0.98$, $p < 0.001$).

Discussion

We demonstrated the possibility of using human movement data, as extracted from Strava Global Heatmap, to quantify functional human disturbance for wildlife over the landscape. We have provided empirical evidence that the cumulated outdoor activity influenced the space use behavior of a Critically Endangered brown bear population (Huber, 2018). Previously, large carnivores have been shown to fear the human 'super predator' (Smith et al., 2017) so that the spatial pattern of human-derived risk perception (Gaynor et al., 2019) can influence large carnivore space use (Cristescu et al., 2013; Ladle et al., 2018) and foraging behavior (Ordiz et al., 2017). A recent human-carnivore coexistence model (Chapron et al., 2014) put forward a community ecology framework where humans are considered as an integral part of the community (Chapron and López-Bao, 2016). Our results support and integrate such a view by demonstrating that carnivore space use is not accurately portrayed when using disturbance metrics that are based solely on structural proxies of human presence (infrastructure *per se*). We showed that the functional use of human structures and presence (i.e. human mobility) provides a more realistic way to address the interplay between carnivore and human use of space.

Functional disturbance outperforms structural variables to predict brown bear habitat selection in Trentino

Peters et al. (2015) showed that bears selected mountainous habitat with forest cover within the home range, and avoided urban areas and linear features linked to human recreation. In this work, we integrated those results by demonstrating that bears avoided specific forms of structural disturbance, as both density (MD4; Table 2) and proximity of man-made infrastructures (MD1, MD3; Table 2) negatively affected bear's space use. Human settlements (e.g. Nellemann et al., 2007; Martin et al., 2010; Peters et al., 2015) and paved roads (e.g. Gibeau et al., 2002; Whittington et al., 2019) had the strongest negative effect as single factors (MD1, MD3; Table 2), whereas trails were mildly attractive (MD3; Table 2), likely because they can be used by animals in moments of low human presence (i.e. night; Tattoni et al., 2015; Oberosler et al., 2017; Ladle et al., 2018). However, it was the cumulative use of landscape by people which drove bear habitat selection within their home ranges (MD5; Table 2). We referred to this effect as functional anthropogenic disturbance, i.e. actual human presence in the landscape. In a community ecology framework (Chapron and López-Bao, 2016), in which humans act as 'super predators' (Tenan et al., 2016; Smith et al., 2017), large carnivores are expected to avoid areas with human-derived risk. If however disturbance occurs in an area of reintroduction, where a newly-established population is still at high risk of local extinction (i.e. Critically Endangered; IUCN, 2001), carnivores may not be able to avoid such risky areas. Bears in our study have demonstrated a good spatial perception of human-derived risk (Gaynor et al., 2019) at the home range scale, scarcely tolerating and thus avoiding large volumes of outdoor non-motorized activities. On the other side, our findings indicate that brown bear is shrinking its ecological niche locally as a result of functional anthropogenic disturbance.

From functional disturbance to functional connectivity: landscape fragmentation from the wildlife's perspective

Metrics of structural disturbance might not be enough to fully understand the implications of human pervasiveness on animal spatial behavior. Not only do humans consume and change the environment, but they also compete directly for space and resources. As a result, their active presence over the landscape could trigger animals' avoidance for suitable spaces (e.g. niche partitioning; Squires et al., 2019). If species have low plasticity or space is limited, direct human competition for space may have serious implications for conservation. Our application of the community ecology-based human-carnivore coexistence model (Chapron et al., 2014; Chapron and López-Bao, 2016) by using a novel metric of functional anthropogenic disturbance indicates that conclusive conservation planning - especially in areas with high human density - should necessarily take into account human mobility. Future applications to other contexts and/or other sensitive large carnivore species (e.g. Amur Tiger, Kerley et al., 2002; Asiatic leopard, Ngoprasert et al., 2007; Iberian lynx, Fernández et al., 2003) could further generalize our findings and their implications for carnivore conservation in a world where human presence is increasingly pervasive, and the community ecology coexistence model will likely be the only viable alternative for their persistence (Chapron and López-Bao, 2016).

We were able to take and demonstrate these concepts into a concrete case of conservation concern. The predictive map (Fig. 2) showed the relative probability of brown bear habitat selection in the area of prime establishment of the reintroduced population. In general, when compared with Peters et al. (2015; Fig. 2a), areas of high probability of use seem to be more distributed, yet more fragmented. Indeed, most of the core habitat patches and linking corridors identified in Peters et al. (2015) correspond in our map to a matrix of suitable, but very small fragments. Our results seem to confirm a certain level of connectivity at the small scale, as previously predicted, but also an important contraction of large suitable areas when we accounted for functional human disturbance. Portions with greater probability of presence were found only in the Central-South Western and Central-Northern sectors of the area, and along some narrow secondary Alpine valleys, whereas extensive human activity and large infrastructures limited the suitability of the main valley bottoms, including Adige valley (Fig. 2).

In light of these findings, the establishment of a long-term, viable Alpine-Dinaric brown bear metapopulation (Kaczensky et al., 2012) may be difficult to achieve, as potential expansion eastwards is still severely limited by both structural and functional anthropogenic disturbance. As bears continue to search for space in this increasingly complex and expanding matrix of anthropogenic disturbance, long term population viability is at risk. To facilitate this expansion, specific measures could be adopted to spatially reduce functional anthropocentric disturbance. Temporal trail/road closure, as well as seasonal restriction of areas, have shown to lower risk of encounters with humans and improved usage of these habitats by wildlife while still providing opportunities for human use (Lamb et al., 2018, Whittington et al., 2019). On the other hand, measures such as the establishment of recreational areas, including protected areas, could have an opposite effect to that desired, as more people would be locally drawn to outdoor activities (e.g. Fredman et al., 2007). The availability of a reliable, yet easy-to-obtain metric of functional anthropogenic disturbance, like the index we developed, is paramount for the effective planning of such mitigation measures.

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Tables and figures

Table 1 - Set of a-priori hypothesis and corresponding models to assess anthropogenic disturbance on brown bear habitat selection at the third-order of selection (within home range). Each a-priori model contained a core set of environmental variables (topography, canopy cover, land use) as predictors and in addition one or more variable(s) for testing anthropogenic disturbance.

ID	Model	Expected disturbance	Covariates
MD1	Aggregate disturbance	Influence of human settlement proximity on selection	Core model + DHS
MD2	Generic linear disturbance	Influence of generic linear infrastructure proximity on selection	Core model + DRT
MD3	Specific linear disturbance	Influence of specific linear infrastructure proximity on selection	Core model + DMR + DFR + DHT
MD4	Density of structural disturbance	Influence of infrastructure network density on selection	Core model + dRTN
MD5	Density of functional disturbance	Influence of human activity density on selection	Core model + dCOI

Table 2 - Output of the set of a-priori models to assess anthropogenic disturbance on brown bear habitat selection at the third-order of selection (see Table 1 for the set of models). The estimated coefficient values (b), the 90% Confidence Interval, and the P-values (*p < 0.01) are reported for each covariate. The models are sorted from left to right based on increasing AIC scores (reported at the bottom).

	Coefficients (90% CI)					
	Model					
	MD5	MD1	MD4	MD3	core	MD2
Slp	2.054*** (1.885, 2.223)	2.394*** (2.228, 2.559)	2.316*** (2.149, 2.482)	2.440*** (2.273, 2.608)	2.626*** (2.463, 2.789)	2.610*** (2.443, 2.776)
TCD	0.831*** (0.759, 0.903)	0.840*** (0.768, 0.912)	0.894*** (0.822, 0.966)	0.924*** (0.843, 1.005)	0.813*** (0.742, 0.884)	0.825*** (0.749, 0.900)
AGR	0.237*** (0.129, 0.345)	0.183*** (0.075, 0.291)	0.028 (-0.077, 0.133)	0.225*** (0.115, 0.336)	-0.078 (-0.181, 0.026)	-0.070 (-0.175, 0.035)
dCOI	-5.048*** (-5.430, -4.667)					
DHS		2.584*** (2.364, 2.803)				
dRTN			-2.587*** (-2.856, -2.319)			
DHT				-0.198*** (-0.286, -0.110)		
DFR				0.057 (-0.044, 0.158)		
DMR				0.935*** (0.828, 1.042)		
DRT						0.530 (-0.608, 1.667)
Constant	-1.699*** (-1.810, -1.589)	-4.438*** (-4.671, -4.204)	-1.879*** (-1.982, -1.776)	-2.771*** (-2.925, -2.617)	-2.083*** (-2.182, -1.985)	-2.099*** (-2.203, -1.995)
Log Likelihood	-13,122	-13,171	-13,286	-13,301	-13,421	-13,420
AIC	26,257	26,354	26,585	26,619	26,852	26,853

Note: *p<0.1; **p<0.05; ***p<0.01

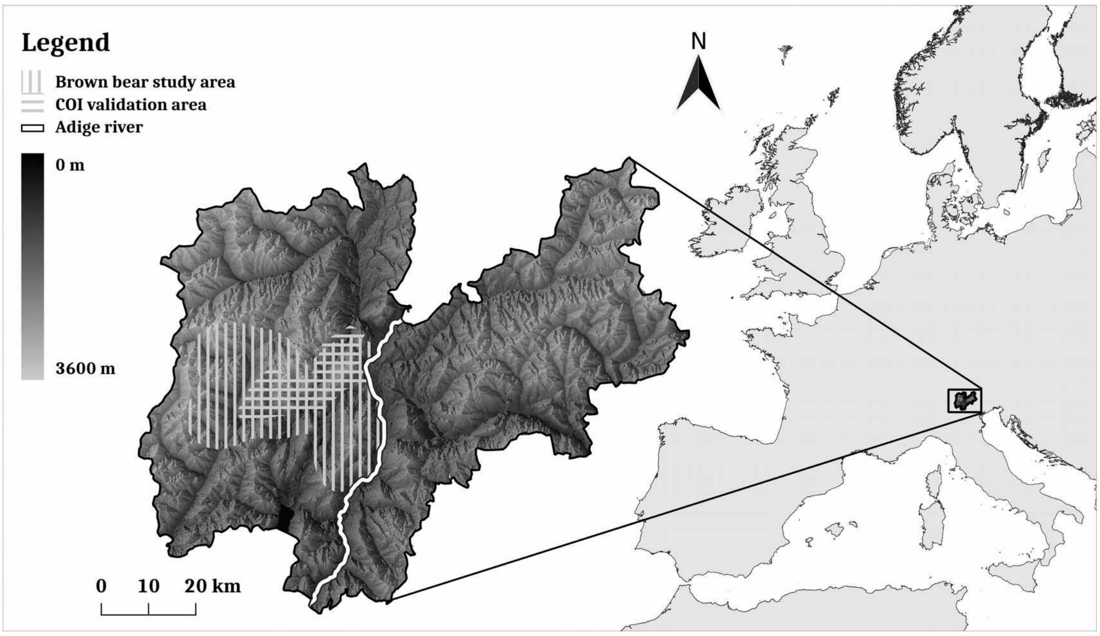

Figure 1 - Digital Terrain Model of the study area. The Adige river watershed divides the area in two sectors: Western and Eastern Trentino. The brown bear area (vertical hatching) is represented by a 95% Kernel Density Estimation of all GPS locations. The area of validation of the Cumulated Outdoor activity Index with ground truth from camera trap observations is indicated by horizontal hatching.

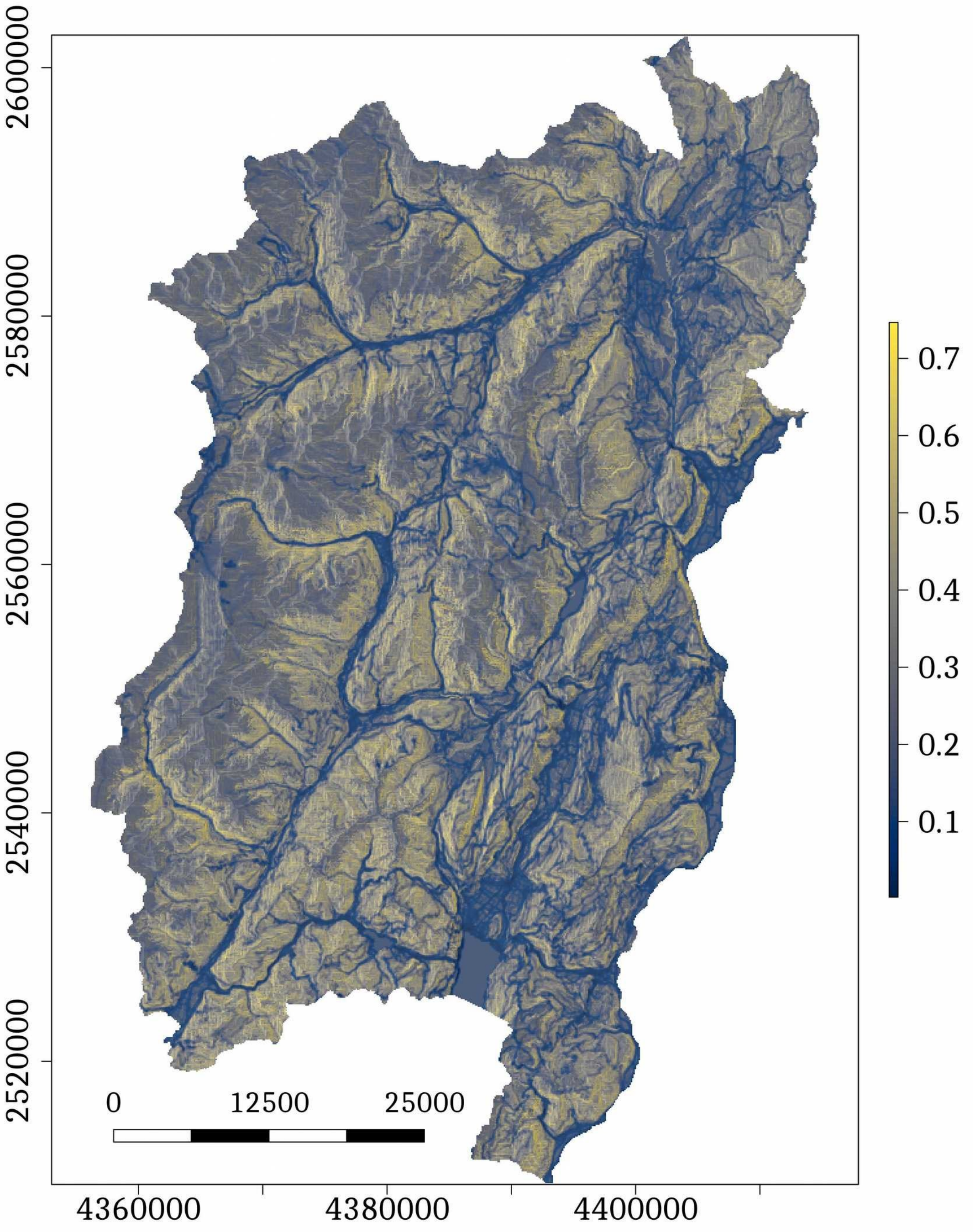

Figure 2 - Predicted relative probability of use by brown bears in Western Trentino, based on third-order (within home range) resource selection coefficients (MD5: slope, tree cover density, cultivated without orchards, density of Cumulative Outdoor activity Index). The map has a resolution of 20 m pixel size.

Supplementary Material

S1. Literature review on Strava applications

We searched "Strava" as topic in the Web of Science online database. We got 35 results as of June 7th, 2019. Among these, 5 had nothing to do with the Strava Application. From the remaining, 26 were articles published in peer-reviewed journals, while 4 were conference papers. Of these, 16 did not use GPS data and mainly used Strava data regarding a) fitness performance (e.g. running/cycling speed, heart beat, running/cycling distance), b) social network usage (e.g. sharing, demographics, social science studies), or c) emerging possibilities by crowdsourced data. The remaining 10 used Strava crowdsourced GPS data, mainly for a) urban planning of cycling ways, b) assess the potential risk of pedestrian and cyclist exposure to traffic accidents and c) assess the exposure of cyclists to urban pollution. All studies have used Strava Metro (Strava, 2018b) data, i.e. the service company linked to Strava app, providing movement data on request. All the articles that used GPS data have been published from 2016 to 2019.

ID	Authors	Year	Topic
1	Lee, Sener	2019	Public health
2	McArthur, Hong	2019	Urban planning
3	Saha, Alluri, Gan, Wu	2019	Risk of bicycle accident
4	Hochmair, Bardin, Ahmouda	2019	Urban planning
5	Boss, Nelson, Winters, Ferster	2018	Urban planning
6	Conrow, Wentz, Nelson, Pettit	2018	Urban planning
7	Sun, Moshfeghi, Liu	2017	Public health
8	Sanders, Frackelton, Gardner, Schneider, Hintze	2017	Urban planning
9	Musakwa, Selaba	2016	Urban planning
10	Jestico, Nelson, Winters	2016	Urban planning

Full reference details

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S2. Technical details on Strava Global Heatmap

The Strava application allows to identify the user track with up to 25 activity types, but the heat rasterization is performed only for four main Activity Types (rides, runs, water, and winter activities). The heatmaps are a static representation of all cumulative activities based upon 2 billion outdoor activity tracks (Strava Press, 2018b), several trillions of GPS locations, and the contribution of tens of millions of active users globally (Robb, 2017). The Strava Global Heatmap (Strava, 2018a) displays the recorded outdoor activity tracks as a ‘pixel path’ connecting consecutive GPS locations (Robb, 2017). To this purpose, the recorded vector tracks (i.e., GPS location series) are rasterized at the resolution of the Web Mercator (EPSG: 3857) tiles at zoom level 16 (OpenStreetMap Wiki contributors, 2019). This zoom level allows tessellation of the world into 2^{16} by 2^{16} tiles each consisting of 256 by 256 pixels, for a final worldwide resolution of 2.3 m per pixel. Each track is defined as a succession of pixel units linking consecutive GPS locations, filtering out stopovers. The resulting average step length of global data is 4 pixels at zoom level 16 (i.e., about 9m). After the rasterization of vectors into pixel paths, a raw heat count is obtained for each pixel by counting all the pixel paths overlapping at that pixel, and normalizing such counts to the bounded range (0, 1) using a Cumulative Distribution Function (CDF). The CDF is computed for each tile (256 x 256 pixels) using all the neighboring tiles over a 5-tiles radius, and further smoothing the transitions between groups of tiles with bi-linear interpolation. The final normalized values are rescaled to a 256 array, thus stored as single bytes, and visualized as a 256-element color spectrum array (Robb, 2017). This procedure is repeated for each zoom level. At lower resolutions, the raw counts are aggregated for each tile (i.e., four tiles become one tile for each lower level of zoom- 1/4th the resolution) and the normalization is recalculated over a 5-tiles radius moving window at the matching scale. The resulting heatmaps have therefore an ordinal measurement level which is valid locally, as they are relative to the level of use of the surrounding space (the 5-tiles radius moving window), and the resolution is degraded at every zoom level, with the lowest level (i.e., zoom 0, resolution= 156412 m/pixel) representing the whole world as a single tile.

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S3. Camera trapping study used as ground truth for the validation of the Cumulative Outdoor activity Index

Oberosler et al (2017) conducted an extensive camera trap survey over an area of 220 km^2 in the southern portion of Brenta (Fig. 1), in the Province of Trento. Between June and August 2015, 60 camera traps were deployed over a predefined systematic grid of 4 km^2 in cell size, adopting the Tropical Ecology Assessment and Monitoring (TEAM) Network protocol (TEAM Network, 2011). The camera traps were distributed across the whole forest altitudinal gradient (500 - 1900 m a.s.l.) to sample wildlife and humans along forest roads and trails (30 sites in each category). Camera traps were placed on a suitable site near the center of each grid cell at an average height of 50 cm and set to take pictures with no delay between consecutive triggers. The sampling period lasted 30 consecutive days in each site, for a total of 1978 camera trapping days and yielded 1514 independent detection events over 58 camera trap stations that functioned well. Humans were recorded either as pedestrians/bikers or vehicles (car, motorbike, tractor, and truck). We considered the former as ground truth observations, and excluded the latter as not matching the purpose of this study.

Literature cited

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S4. Statement on animal subjects

In Italy, the brown bear is currently protected under European (Habitats Directive 92/43/EEC, incorporated in the Italian legislation via D.P.R. 357/97) and Italian Laws (L. 157/92), and included as a strictly protected species in the Bern Convention (1979). Under derogation of the aforementioned Habitat Directive, approved by the Italian Institute for Environmental Protection and Research (ISPRA), it is permitted to capture animals for research, public safety, and damage prevention purposes. Within these limits, all trapping and handling operations of wild brown bears are regulated by the "Interregional action plan for the conservation of the brown bear in the central-eastern Alps" (PACOBACE, 2010), approved by Directorial Decree n. 1810 of 5 November 2008 and amended by Directorial Decree Protocol 0015137 PNM of 30 July 2015.

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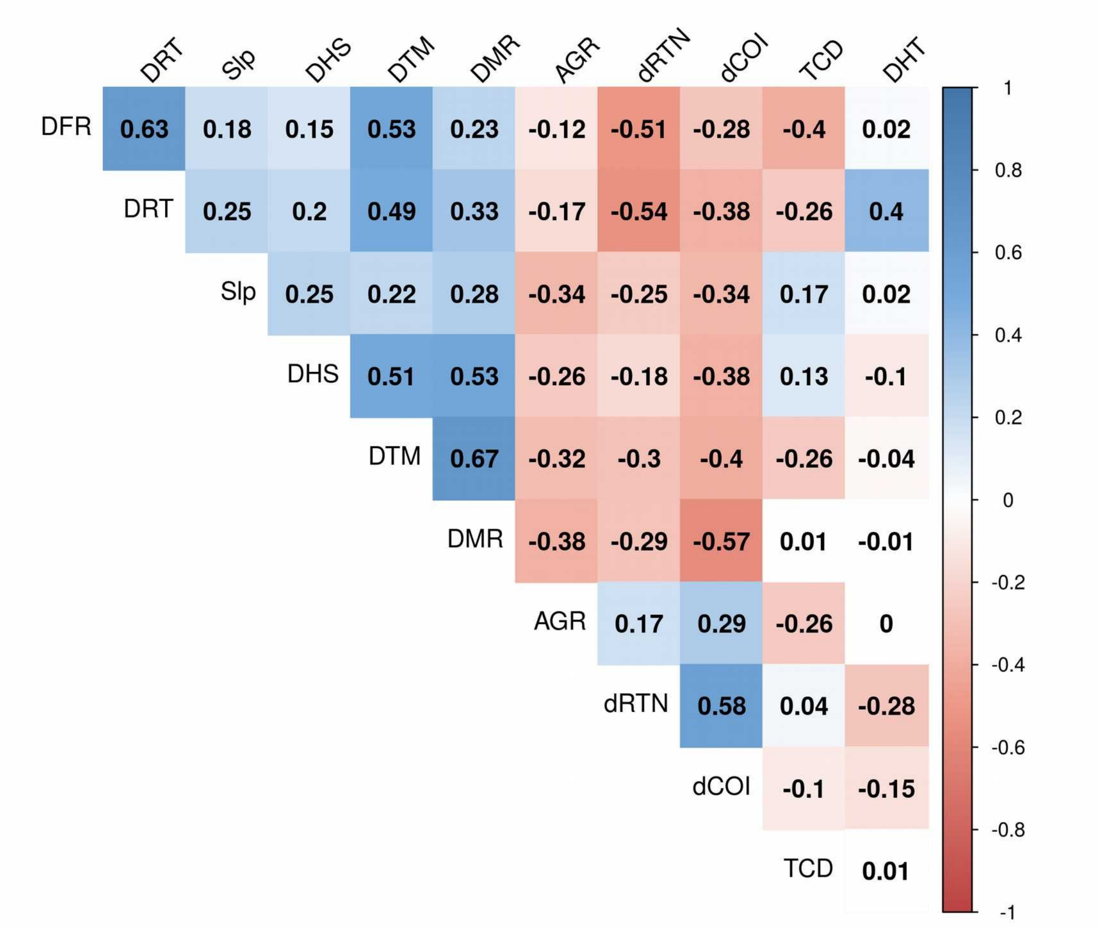
S5. Description and correlation analysis of spatial covariates

We identified a set of topographic, land use and anthropic disturbance variables as spatial predictors initially selected for the RSA (see Material and Methods, Resource Selection Analysis). For each covariate the acronym used in the analysis, the description, the original unit, and the source are reported. All the environmental layers were resampled to a common origin (WGS 84/Pseudo-Mercator Coordinate systems; EPSG: 3857) and resolution of 20 m. All variables (see Material and Methods, Environmental layers) were checked for collinearity.

Table S5.1 - Selected spatial covariates measuring environmental features and different forms of anthropogenic disturbance used in the RSF models. The covariates above the dashed lines are the core environmental variables, while those below are the anthropogenic disturbance variables. For the full reference details, see Literature cited.

Covariate	**Description**	**Unit**	**Original Resolution**	**Source**
DTM	Digital Terrain Model	Meter	2 m	LiDAR
Slp	Slope	Radians	2 m	LiDAR
TCD	Tree Cover Density	%	20 m	High Resolution layer, Copernicus Programme
AGR	Cultivated (without orchards)	Class	Polygons	CORINE Land Cover, Copernicus Programme
DHS	Distance from Human Settlements	Meter	Polygons	CORINE Land Cover, Copernicus Programme
DMR	Distance from Main Roads	Meter	Polygons	Autonomous Province of Trento
DFR	Distance from Forest Roads	Meter	Polygons	GeoCatalogo PAT
DHT	Distance from Human Trails	Meter	Polygons	GeoCatalogo PAT
DRT	Distance from Roads and Trails	Meter	Polygons	Autonomous Province of Trento; GeoCatalogo PAT
dRTN	density Road and Trail Network	Class	Polygons	Autonomous Province of Trento; GeoCatalogo PAT
dCOI	density COI	Index	20 m	*Proposed*



	DRT	Slp	DHS	DTM	DMR	AGR	dRTN	dCOI	TCD	DHT
DFR	0.63	0.18	0.15	0.53	0.23	-0.12	-0.51	-0.28	-0.4	0.02
DRT		0.25	0.2	0.49	0.33	-0.17	-0.54	-0.38	-0.26	0.4
Slp			0.25	0.22	0.28	-0.34	-0.25	-0.34	0.17	0.02
DHS				0.51	0.53	-0.26	-0.18	-0.38	0.13	-0.1
DTM					0.67	-0.32	-0.3	-0.4	-0.26	-0.04
DMR						-0.38	-0.29	-0.57	0.01	-0.01
AGR							0.17	0.29	-0.26	0
dRTN								0.58	0.04	-0.28
dCOI									-0.1	-0.15
TCD										0.01

Figure S5.1 - Correlation matrix with the Pearson correlation coefficients between each variable. Positive correlations are displayed in blue, while negative correlations in red. Color intensity is proportional to the correlation coefficient.

Literature cite

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S6. Correlation between the Cumulated Outdoor activity Index and human detection events obtained via camera traps

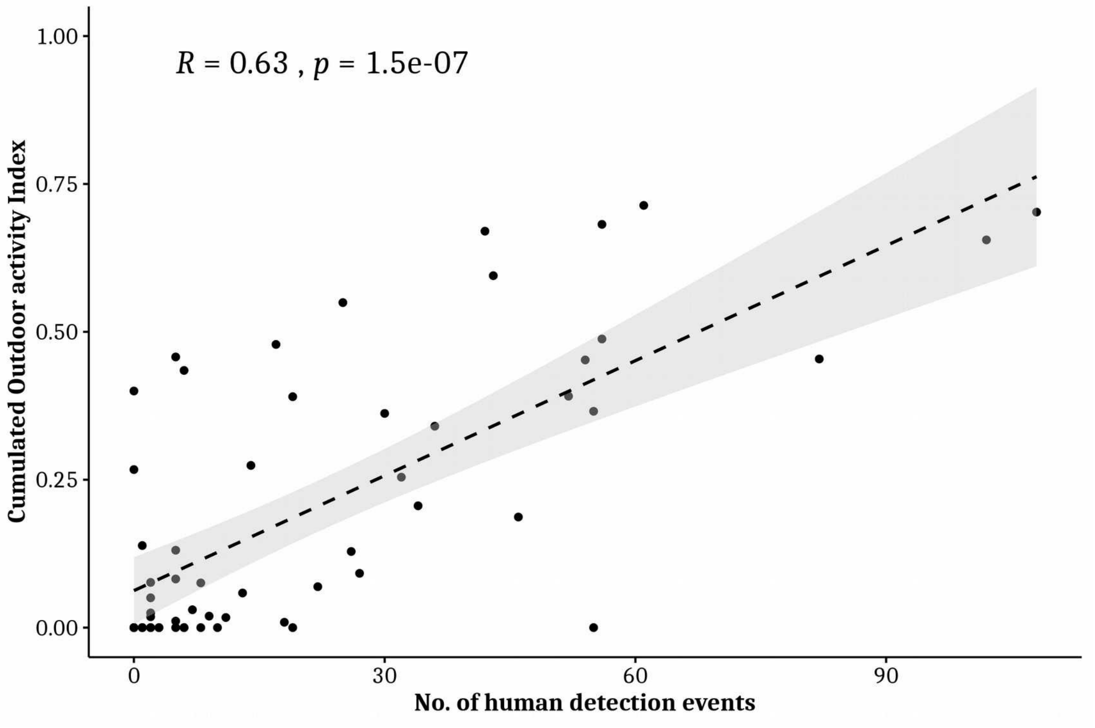

Figure S6.1 - Correlation between the newly-derived Cumulative Outdoor activity Index and number of human detection events with the camera trapping survey. The regression line (dashed line with 95% confidence interval) is represented along the raw data (dots).

S7. Individual bear's annual home-range

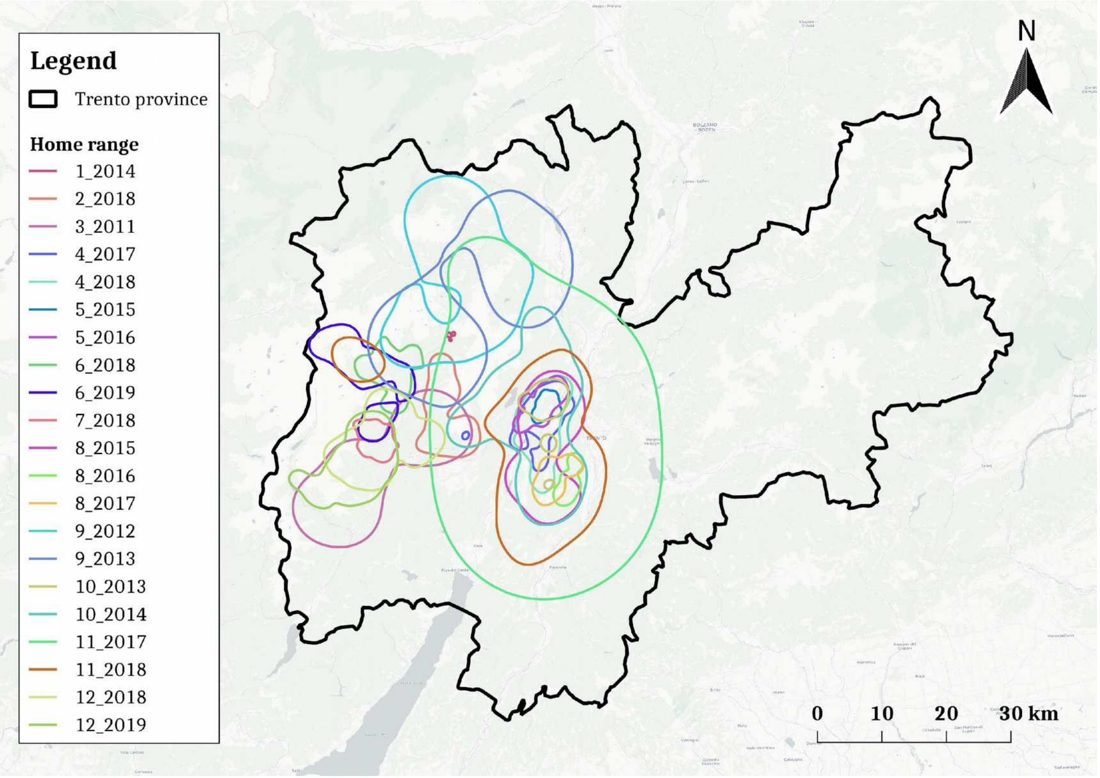

Figure S7.1 - Individual bear's annual 90% fixed kernel home-range in the province of Trento. The brown bear home ranges are represented by colored polygons. The mean home range size (animal/year) was 259.51 km^2 (IQR 40.50 km^2 to 313.43 km^2).

Chapter 2

Human-induced risk affects the ecological niche of brown bears in the Central Alps

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The manuscript is in preparation for submission

Abstract

Even the largest terrestrial carnivore of mainland Europe, the brown bear, must adapt to human presence; its movement, behavior, and diet are largely influenced by humans. The analysis of brown bear movement data has shown that bears perceive human-related risk differently in relation to human activity level, season and time of day, and employ a security-food trade-off strategy. In a human-dominated landscape, when displacement is not an option because of habitat limitations and social mechanisms (such as female philopatry), bear mobility may clash with human activity, thus generating conflict and decrease in acceptance. Brown bears' ability to cope with risky situations is particularly reduced during "biologically sensitive" periods (i.e. resting, mating, or fattening up for hibernation), therefore the selection of suitable areas where to fulfill these basic needs is crucial for the long-term survival of individuals. In this study, we measured multi-scale response to risk perception and food resource proximity by examining the selection of home ranges (‘large-scale’) and bedding locations (‘fine-scale’) of GPS-tagged brown bears in a highly heterogeneous human-dominated landscape. Resting locations were identified with an *ad-hoc* spatio-temporal cluster analysis, which has been later validated through field investigations. Food resources were mapped using a GIS-database including spatial and non-spatial ecological information on fruiting plants in the study area, and risk perception was derived from human mobility data. We observed that brown bears in the Alps apply a security-food trade-off strategy, balancing their need for food resources against anthropogenic disturbance at various scales. In a community ecology framework, human "super-predator" altered the bear's fundamental and realized niche. While the spatial predictions indicated that suitable areas exist, we propose that human access be restricted during "biologically sensitive" periods to ensure the long-term survival of individuals.

Keywords: Ecological niche; Risk perception; Anthropogenic disturbance; *Ursus arctos*; Strava

Introduction

As land use by humans increases dramatically around the world (Foley et al., 2005) and recreational activities spread beyond urban contexts (Knight and Gutzwiller, 1995), spatial overlap between humans and wildlife has intensified, leaving even less undisturbed areas for animal use. Competition for space emerges through both potential (i.e. structural) and actual (i.e. functional) presence of humans in the landscape (Corradini et al., 2021; Nickel et al., 2020), forcing a growing number of species to make behavioral adaptations to both anthropic environmental changes (Tuomainen and Candolin, 2011) and direct risk (i.e. human-caused mortality; Creel and Christianson, 2008). When competition with humans for space or resources emerges, animals may respond by displacing into safer and less disturbed habitats (Martin et al., 2010) or adjusting their activity cycles (Gaynor et al., 2018), or both (Schuette et al., 2013). Fear of humans can change diel activity patterns in large herbivores (Bonnot et al., 2019) or reduce feeding time in medium-sized (Suraci et al., 2019) and large carnivores (Smith et al., 2017). Understanding how species respond to anthropogenic disturbance is becoming central in ecology and conservation (Rutz et al., 2020), yet is hindered by scale-dependent observations (Levin, 1992). Disentangling spatio-temporal responses to risk perception and competition can provide important insight into animal well-being, species conservation, and landscape dynamics (Suraci et al., 2019).

Applying a community ecology framework to a human-disturbed region, in which human “super predators” (Smith et al., 2017) are regarded as an integral part of the ecosystem (Chapron and López-Bao, 2016), large carnivores could coexist with humans only by modifying their diet, movement, and behavior- echoing a predator-prey response (i.e., risk effect, Creel and Christianson, 2008). Specific research exploring the spatial requirements for carnivores during “biologically sensitive” periods (i.e. resting, mating, or fattening up for hibernation; *sensu* Yovovich et al., 2020) should provide a robust evaluation of risk perception. For instance, the ability to cope with risky situations is minimal during moments of lowest mobility (i.e. at rest; Lima et al., 2005), making animals particularly vulnerable to risk when asleep (Cristescu et al., 2013). Moreover, for certain species, such as hibernators, enough food intake is essential at certain times of the year (i.e. hyperphagia). A human-induced landscape of fear can compromise access to these resources (Lodberg-Holm et al., 2019), which may in turn jeopardize individual survival if disturbance is high. Understanding how species respond to competition and risk (Gaynor et al., 2019) and how they adapt to human disturbance during these “biologically sensitive” moments is pivotal for the long-term conservation of carnivores and the whole ecosystem (Ripple et al., 2014).

Unlike a singular behavioral adaptation, demonstrating a multi-scale fear response in a large carnivore effectively demonstrates the shrinking of its realized niche, and therefore reduction in its functional ecological capacity- both as individuals within a population and within a community.

Despite the recent increase in the Alpine bear population (Groff et al., 2020), anthropogenic mortality still appears to drive adult survival and population dynamics (Tenan et al., 2016), making humans function ecologically as a “super-predator” (Smith et al., 2017). Furthermore, previous work on bears’ behavioral reaction to encounters with humans showed a prevalent fear of people (Moen et al., 2012), suggesting that individuals perceived human-derived risk and adopted behavioral strategies to reduce risk exposure (i.e. antipredator response; Gaynor et al., 2019). Despite the importance of assessing the risk effect in bears and large carnivores in general, rarely has a multi-scale approach been applied (Suraci et al., 2019). Furthermore, structural and functional disturbance components (Corradini et al., 2021), which in turn affect resource utilization capacity, are rarely disentangled and assessed to understand how humans impact the species’ niche. It is crucial to consider that the relative effect of anthropogenic disturbance varies by observation scale (Levin, 1992), meaning that ecological patterns (e.g. limiting factors) could only emerge at specific scales of inference (i.e. Ciarniello et al., 2007), leading to deceptive decision-making processes when evaluating anthropogenic disturbances. A multi-scale, spatio-temporal evaluation of human-derived risk responses could help assess the implications of sharing the landscape with humans and understand how to mitigate conflict to promote species recovery. The Alpine brown-bear population, listed as Critically Endangered (Huber, 2018), therefore represents an ideal case-study to disentangle large carnivore behavioral responses to multiple anthropogenic disturbance and risk factors.

In this study, we assess behavioral responses of bears to risk and resource availability at two ecologically relevant scales: home range (“large-scale”) and resting locations (“fine-scale”). We focused on the influence of anthropogenic disturbance during several “biologically sensitive” periods, that is, those physiological and behavioral states in which exposure to human-derived risk could have a particularly negative impact on brown bears. Using the Alpine bear as a case study, we tested two main hypotheses: (i; “large-scale”) when selecting for home ranges, bears must weigh their need for resources against risk perception across seasonally variable energetic requirement periods. For this purpose, we modeled bears’ fear response by resource selection accounting for functional anthropogenic disturbance (i.e. COI; Corradini et al, 2020) and resource availability (i.e. Tattoni et al., 2019) according to the main biological phases (hypophagia, mating season, and hyperphagia). We predicted that risk perception mainly drives resource selection of bears throughout the year, forcing individuals to apply a trade-off strategy during “biologically sensitive” periods (i.e., hypophagia and hyperphagia, two physiologically important stages, as well as mating) in order to reduce risk exposure while in proximity of resources; (ii; “fine-scale”) when selecting for resting sites, bears shall select sites in areas with low functional anthropogenic disturbance to the detriment of resource proximity. For this purpose, we modeled the individual selection of resting sites by countering human-derived risk perception, forest canopy structure, and resource availability. We predicted that bears maximize protection during moments of highest vulnerability (i.e. resting, another important “biologically sensitive” period) by applying a security-food trade-off strategy (Cristescu et al., 2013) that avoids functional anthropogenic disturbance and seeks more concealment due to perception of risk over resource proximity. Such findings would support the assumption that bears living in a human-dominated environment would, as a result of multi-scale response to risk perception and anthropogenic disturbance, compromise the selection of resources and ultimately reduce their realized niche.

Materials and methods

Study area

The research was conducted in the province of Trento (10.5° E, 45.6° N - 12.0° E, 46.5° N), a mountainous region in the Central-Eastern Italian Alps (Figure 1). The area covers 6.200 km^2 in the Alpine biogeographical region (EEA, 2002) and is characterized by a complex set of microclimates due to a morphologically diverse landscape (from 65 to 3769 m a.s.l.). The territory is largely covered by forests and prairies according to the altitudinal succession, while valleys are largely human-dominated (87 inhabitants/km^2). The Adige valley, the largest and most developed of the region, poses a major threat to ecological connectivity for many animal species (Figure 1).

The local brown bear population is the result of a reintroduction project in which 10 adult bears from Slovenia were released in the Adamello Brenta Nature Park, Italy, between 1999 and 2002 (PACOBACE, 2010). The population has settled in Western Trentino and is currently estimated to be around 90 individuals (Groff et al., 2020). However, despite a numerical increase since the first releases, the Alpine population is currently listed as Critically Endangered due to the small number of mature individuals (< 50, Criteria D1; IUCN, 2001) (Huber, 2018). Brown bears are legally protected under European (Habitats

Directive 92/43/EEC) and Italian (L. 157/92) laws, except for the removal of bears which are deemed dangerous (PACOBACE, 2010).

Brown bear movement data

Between 2006 and 2019, 18 adult bears (11 female and 7 male) throughout the study area were captured and fit with GPS collars (Vectronic Aerospace GmbH, Berlin, Germany) as part of the monitoring programme carried out by the Autonomous Province of Trento (PACOBACE, 2010; Supporting Information S1 for animals capture details and protocols). Bears were tracked on the basis of management needs from one to several years, for a total of 44 animal/year. GPS collar acquisition intervals varied between individuals, therefore we used different resolutions (6-hour and 3-hour sampling protocol) based on the type of ecological question we wanted to answer. We used regular time interval trajectories (i.e., bursts) for each prediction. For the first prediction (“large-scale”), higher-resolution movement bursts (those with a sampling protocol equal to a submultiple of 6) were down-sampled to match the desired sampling protocol. For the second prediction (“small scale”), we discarded lower-resolution movement bursts (e.g., 6-hour sampling protocol) and down-sampled higher-resolution movement bursts to have consistent 3-hour intervals. Data quality assessment was done following the procedure presented by Urbano et al (2014), therefore only ‘valid locations’ were retained for the analysis. Specifically, we removed all the locations with no, duplicate, or impossible timestamp. Locations in impossible places (for example, a lake or outside the study area), locations displaying impossible (based on possible speed) or suspicious (based on “spikes”) movement, and locations with a poor degree of reliability (DOP > 10) were also deleted. Lastly, we subsetted the trajectories by only considering the non-hibernating period, resulting in a dataset consisting of GPS positions from April 1st to October 31st.

High-resolution predictor variables

Field measurements are challenging in Alpine environments, therefore we opted for high-resolution remote sensed data to avoid biases imposed by the inaccessibility of GPS locations and to render large-scale spatial predictions. Based on our research questions and knowledge of the ecological context, we extracted meaningful spatial information from a combination of space-, air- and human-borne sensors at the highest resolution available (Supporting Information S3 for the detailed description of spatial covariates; Table S3.1).

We accounted for topographical variability by deriving the slope from LiDAR-derived Digital Elevation Model. We derived the forest canopy structure as both vertical (i.e. Canopy Height Model; *CHM*) and horizontal (i.e. Tree Cover Density; *TCD*) cover and used the monthly Enhanced Vegetation Index (*EVI*) as a proxy of vegetation productivity. We derived the fruit availability (*r-berry*) of 44 plant species commonly eaten or considered edible for the brown bears (Table S3.3) based on the GIS approach developed by Tattoni et al (2019). 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 scales. Lastly, in order to depict a realistic spatial pattern of risk perception (Gaynor et al., 2019), we included human mobility data (i.e. proxy of functional anthropogenic disturbance) as the density of the newly-derived Cumulated Outdoor activity Index (*dCOI*; Corradini et al., 2021). All raster layers had a spatial resolution of 20m and were normalized by subtracting the mean and dividing by its standard deviation. We managed, processed, and analyze 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, United Kingdom).

Space use and resource selection ("large-scale")

We modeled the selection of home ranges across the population range, i.e. second-order selection scale (Johnson, 1980), via Resource Selection Function (RSF). The 90% Utilization Distribution (Worton, 1989; Calenge, 2006) derived from GPS locations from at least a 6-hour sampling protocol was identified as the individual home range. We estimated selection using a used/available design (Manly et al., 2002) and fit Generalized Linear Mixed Model (GLMM) with a binomial error distribution via maximum likelihood, using a Laplace approximation. We included spatial covariates as additive fixed terms, sampling five times as many resource units available as the used GPS-based locations. We included individuals as random intercepts in the model in order to account for among-individual variability and to account for unbalanced sample designs and autocorrelation (Gillies et al., 2006). For the purpose of the study, we estimated marginal (population-level) responses only. Building on previous findings from Peters et al (2015) and Corradini et al (2021), we fit monthly ecologically meaningful models including non-collinear covariates. We thus included the slope (as both linear and quadratic effect) and the density of COI as static variables, while the EVI and species richness of fruiting plants as dynamic (i.e. time-varying) variables. In order to understand the relationship between space use and selection of resources based on human-derived disturbance, we included in the model the interaction between the species richness of fruiting plants and the density of COI. For each monthly model, we assessed whether to consider the additive terms alone or together with the interaction effect based on the Analysis of variance (ANOVA). We analyzed the seasonal differences by considering the main physiological/behavioral states of brown bears: (i) hypophagia 1 April - 31 May, (ii) mating season 1 June - 31 July, and (iii) hyperphagia 1 August- 30 October (Ciucci et al., 2014).

Resting site selection ("fine-scale")

Identification of bedding sites

Bedding sites were identified via spatiotemporal clustering of GPS animal locations from a 3-hour sampling protocol. Through functions provided by the R package "recurse" (Bracis et al., 2018), we identified hotspots of use (i.e. clusters) based on ad hoc parameterization. First, for each GPS location, a circle of 25 m radius was drawn and the number of the other GPS locations within that circle was counted. Next, we categorized every cluster as 'bedsite' when it included locations for at least 9 consecutive hours (Figure S2.1). We chose a detection radius of 25 m to account for GPS measurement error and a time interval larger than 9 hours to reduce the detection of non-target hotspots (i.e. foraging areas) while having a consistent detection even in case of missing values (i.e. missing values for sites under dense canopy cover). Then, we calculated the centroid for each detected cluster and discarded any revisits to reduce autocorrelation problems. Last, we performed field validation to assess the ability to detect bedsites based on an ecologically and technologically meaningful parameterization (Supporting Information S2 for specifications on field validation).

Statistical analysis

We considered the selection of resting (bedding) sites as a discrete choice influenced by movement, therefore we opted for a matched case-control approach where each bedsite location is matched with a conditional availability set. 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 bedsite (i.e. case), which represented a stratum, was paired with 25 random points (i.e. controls) generated by resampling turning angles and step lengths from the empirical distribution (Fortin et al., 2005) of bear 3-hour step length. We used this resolution to parameterize the available points in order to obtain fine-scale selection. In order to best approximate their distributions, we fitted different univariate distributions by maximum likelihood estimation and selected the best distribution by conducting a Goodness of Fit test using the R package "fitdistrplus" (Delignette-Muller & Dutang, 2018). We thus linked individual selection of resting sites to available habitats by taking into account environmental features and anthropogenic disturbance. We included slope (linear and quadratic effect) as a proxy of topographic variability, TCD and CHM as a proxy of horizontal and vertical canopy cover of forest respectively, the density of COI as a proxy of functional anthropogenic disturbance, and the monthly species richness of fruiting plants as a proxy of food resources. We included again the interaction effect between resource selection and human-derived disturbance. We excluded EVI because the resolution was too coarse (250 m) for fine-scale analysis. The selected spatial covariates were included as fixed additive terms, while individuals were treated as random slopes in the model with respect to anthropogenic disturbance to account for among-individual variability.

We calculated the relative probability of using a given location as a bedsite, based on selection coefficients from the best fitting model. We discarded the time-varying covariate in order to derive a static, year-round prediction map. We tested 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

Space use and resource selection ("large-scale")

We used the 6-hour GPS frequency position from 12 animals (8 females and 4 males) for a total of 21 animals/year. Due to the lack of variability in species richness of fruiting plants, we discarded the model for April. In general, brown bears selected their home ranges in high-productivity sites, with steep terrain and high fruit diversity, while avoiding areas with a high density of functional human disturbance. The vegetation productivity was the predictor with the largest effect size for all months than any other covariate (b_{EVI}= +0.528 to +0.975, $p < 0.001$; Table 1). Similarly, bears selected for areas with high species richness of fruiting plants, except in August, but to a lesser degree than EVI ($b_{r\text{-}berry}$= +0.124 to +0.292, $p < 0.01$ to $p < 0.001$; Table 1). On the other hand, bears strongly avoided areas with a high density of functional disturbance constantly throughout the year (b_{dCOI}= -0.462 to -0.690, $p < 0.001$; Table 1). Interestingly, the carnivore displayed specific responses during the various physiological states when considering the relationship effect between functional human disturbance and species richness of the fruiting plants ($b_{dCOI:r\text{-}berry}$= -0.138 to -0.218 when there is a significant relationship, $p < 0.05$ to $p < 0.001$; Table 1). As shown by the ANOVA, the additive and interaction effects together led to more parsimonious models in June, August, September, and October (Table S5.1), while the interaction effect was not significant in May and July (Table 1; Table S5.1). Topographical variability was also an important predictor, as bears selected for steep areas (b_{Slp}= +0.276 to +0.564, $p < 0.001$; Table 1), but avoiding extreme slope values in certain months ($b_{Slp\char`^2}$= -0.066 to -0.153 when there is a significant relationship, $p < 0.05$ to $p < 0.001$; Table 1).

Resting site selection ("fine-scale")

Through the spatiotemporal clustering of GPS bear locations, we were able to classify a total of 1011 bedsites, of which 557 were selected for analysis because they overlapped in space (i.e., Western Trentino; Figure 1) and time (i.e., between May to October) with the environmental predictor variables. Bears primarily selected their resting sites in areas with a low density of functional anthropogenic disturbance (b_{dCOI}= -0.752, $p < 0.001$; Figure 2; Table 2), more so than any other spatial covariate as the effect size of dCOI was the largest of the candidate model. Bears also selected for resting sites under higher horizontal (b_{TCD}= +0.412, $p < 0.001$; Figure 2; Table 2) and lower vertical canopy cover (b_{CHM}= -0.308, $p < 0.001$; Figure 2; Table 2). Slope was positively selected as a linear effect (b_{Slp}= +0.241, $p < 0.01$; Figure 2; Table 2), but not when included as a quadratic term ($b_{Slp\char`^2}$= -0.067, $p > 0.05$; Table 2). Importantly, the availability of resources did not significantly affect the selection of resting sites, as shown either as a single 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 (Figure 4) was obtained including only the significant terms, namely Slp, TCD, CHM, and dCOI (Figure 2) . The k-fold cross-validation showed that the best fitting 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

We demonstrated that brown bears in the Alps apply behavioral strategies to reduce human-derived risk exposure. By analyzing their movement data in combination with time-varying, high-resolution spatial information, we showed that bears avoid functional anthropogenic disturbance while selecting areas with higher wild fruit availability and higher vegetation productivity. Furthermore, bears showed to weigh their need for various resources against anthropogenic disturbance during the main dietary phases. By analyzing the distribution of resting sites, we also found that the overall perception of risk has influenced site selection more than available resources, supporting evidence that the predator applied a trade-off strategy to reduce risk while accessing large scale resources. These results showed that humans, as the largest predator and competitor in the ecosystem, played a primary role in modifying space use, resting patterns, and foraging behavior of the Alpine brown bear. In a community ecology framework (Chapron and López-Bao, 2016), the ecological niche of the bear was reduced due both to risk perception (i.e. predation) and habitat competition.

Risk perception drives the selection of space, resource and resting site in Alpine bears

Previous studies (Preatoni et al., 2005; Peters et al., 2015) have shown that the Alpine bear has a tendency to avoid proximity to human settlements and infrastructure. Furthermore, we have recently demonstrated by including human mobility data that functional anthropogenic disturbance primarily drives selection within the home ranges (Corradini et al., 2021). Our results complement those findings by showing that bears similarly select their home ranges in areas with low anthropogenic disturbance while choosing for high vegetation productivity and steep terrains independently of seasonal behavioral states. Intuitively, since proxies of disturbance from human infrastructure and land use might be inadequate to represent risk distribution (Corradini et al., 2021), human mobility provided an ecologically meaningful ‘landscape of fear’ (Gaynor et al., 2019).

The presence of people in the environment forced bears to balance access to resources and mating opportunities while accounting for risk. The carnivore selected locations with a higher richness of fruiting plants in relation to disturbance almost all year round, supporting the hypothesis that it applied a security-food trade-off strategy (*sensu* Cristescu et al., 2013). During hyperphagia, when highly caloric food is needed for accumulating fat for winter denning, fleshy fruits represent an important food source for bears (Ciucci et al., 2014). Areas with higher fruit richness were selected because they provided predictable and profitable food sources, which are especially important when establishing a home range. However, when anthropogenic risk perception was high, the species richness of available fruits decreased in importance in space use selection. These findings showed that perceived risk could have negative consequences to fitness through an increase in risk effects (Creel and Christianson, 2008), as bears reduced the time spent in food-rich areas when the functional anthropogenic disturbance was high (Figure 2). Importantly, brown bears were only partially found to limit resource access during the central months of the mating season (1 June - 31 July; Ciucci et al., 2014) when anthropogenic risk perception was high (Table 1). This could be because individuals may need to access resources in the short term to offset the effort of breeding following the peak of mating season (June). Nonetheless, during the breeding season, areas with a high human presence were always avoided, demonstrating how anthropogenic risk perception may influence mating opportunities in this population.

Previous research on bear activity patterns (Oberosler et al., 2017), assessed by systematic camera trapping, showed a tendency to minimize human-derived risk by reducing daytime activity. Although shifting activity can decrease the risk of interaction while foraging, it increases vulnerability during moments of reduced capacity to detect and cope with risky situations (i.e. resting). For this reason, bedding site selection is another important determinant of predation risk perception (i.e. 'where to sleep'; Lima et al., 2005), as animals spend most of their lives in this vulnerable behavioral state. In our research, we have shown that risk aversion primarily influenced the selection by brown bears as individuals selected sites with reduced human mobility, in steep areas (likely perceived as safer than surrounding areas; Martin et al., 2010), and with denser canopy cover (which provided more concealment and possibly thermal comfort; Lima et al., 2005). Alternatively, it was found that proximity to productive feeding areas was not relevant at rest, as our findings suggested that bears maximize individual security over food intake (Cristescu et al., 2013). The predictive map showed where bears were more likely to rest in Western Trentino (Figure 4). The map illustrated that large, suitable contiguous areas were to the west, while greater fragmentation and less suitability to the east limited the availability of resting sites. Interestingly, the portions of the study area with the highest relative probability were found in the South-Western sector, where few bears are present at the moment (Groff et al., 2020). The intense human activity in the major Alpine valleys greatly limited the number of suitable sites, whereas wooded mountain portions could provide shelter areas for bears.

Humans potentially shape bear's realized and fundamental 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 and Le Lay, 2008). We recognize that numerous definitions of ecological niche exist (see review from Pocheville, 2015), as well as the fact that the niche has a very large number of dimensions (Polechová and Storch, 2008), making exact quantitative measurement nearly impossible. However, as pointed out by Pocheville (2015, pp. 575): "*[...] its multiple [niche] meanings all revolve around the Darwinian view of ecosystems that are structured by the struggle for survival*", we decided to embrace this concept and refer to 'niche' in the broadest sense of species persistence.

The spatial variation in predation risk (Gaynor et al., 2019) as depicted by human mobility data showed that human 'super-predator' (Smith et al., 2017) influence bear's space use, resource and resting site selection, similar to what one would expect in a community ecology framework (Chapron and López-Bao, 2016). Therefore it is ecologically reasonable to assert that humans alter the bear's realized niche through interspecific interactions (i.e. predation and competition; Hutchinson, 1957). As a consequence, the reduced ecological function of the brown bear may mean that the ecological effectiveness of such a reintroduced population will have limited impact on community dynamics and structure in the Alps, thereby mitigating reintroduction programme success.

Furthermore, the profound changes in the ecosystems created by humans decrease both the availability and the reachability of (environmentally) suitable ecosystems. For instance, even in the complete absence of biotic interactions (i.e. inter- and intraspecific), certain abiotic determinants (e.g. extreme orography, cemented soils, or structural barriers) would remain standing and would not allow a species to persist. Humans are the world's primary ecosystem engineers (Root-Bernstein and 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 favorable conditions of species (i.e. fundamental niche; Hutchinson, 1957) even before ecological interactions are taken into account. Despite, strictly speaking, fundamental niches are inestimable (Panzacchi, et al., 2015), their approximation can still provide valuable information on a species' potential distribution and its tolerance to external changes. In the Alpine environment, because such changes have undergone for centuries or even millennia, we would suggest that humans engineered the ecosystem in such a dramatic way to have redefined the fundamental niches of species. Additional research, conducted at the proper scale (Alpine-Dinaric), may give a more holistic knowledge of humans' influence on the Alpine ecosystem, and therefore on the brown bear.

Implications on coexistence

The coexistence level between humans and bears in the Alpine region is currently "weak" (Chapron and López-Bao, 2016), with the latter being ecologically excluded in areas with a high level of conflict. Besides, despite the population having increased in the years after reintroduction (Groff et al., 2020), anthropogenic mortality drives adult survival and hence population dynamics (Tenan et al., 2016). Without major socio-ecological changes, the availability of suitable habitats for bears will inevitably decline in the years to come (e.g. Steffen et al., 2015). When displacement is not an option because of habitat limitations (i.e. connectivity) and social mechanisms (such as female philopatry), bear mobility could increasingly clash with human activity, thus generating conflict and a decrease in acceptance. Some authors argued (Tattoni et al., 2017) that the good publicity derived from the presence of the bear can contribute to develop a positive bond with the local population and help to reduce conflicts but this can be only a small piece in a complex mosaic. With the increase of (ecological) interactions, removal of bears for management and by poaching could increase (Tenan et al., 2016), reversing the positive population growth and potentially jeopardizing the long-term survival of the Alpine-Dinaric brown bear meta-population (Kaczensky et al., 2012). In this context, understanding risk perception in wildlife can allow mitigation of anthropogenic risk, with benefits to long-term animal fitness. Using the high-resolution spatial predictions (20 m pixel size), specific measures to limit anthropogenic disturbance during vulnerable moments (i.e., at rest and during "biologically sensitive" periods) could be implemented. For example, restricting access to highly sensitive areas during the day (> 0.75 projected probability; Figure 2) and during the final weeks of the fattening season, when bears have the highest energy requirements (i.e. October), could reduce the impact of perceived risk. Access rules have been successfully implemented in other socio-ecological contexts (e.g., Bear Management Areas in Yellowstone National Park, Coleman et al., 2013; or motorized access controls in Canada, Proctor et al., 2020), and they can be reapplied locally with the goal of balancing bear conservation and human recreation. We want to emphasize that, despite the challenges of achieving high levels of coexistence in certain landscapes, particularly those that are heavily populated by humans (Chapron and López-Bao, 2016), timely and spatially-explicit mitigation efforts could still ensure the survival of brown bears in the Central Alps for decades to come.

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Tables and figures

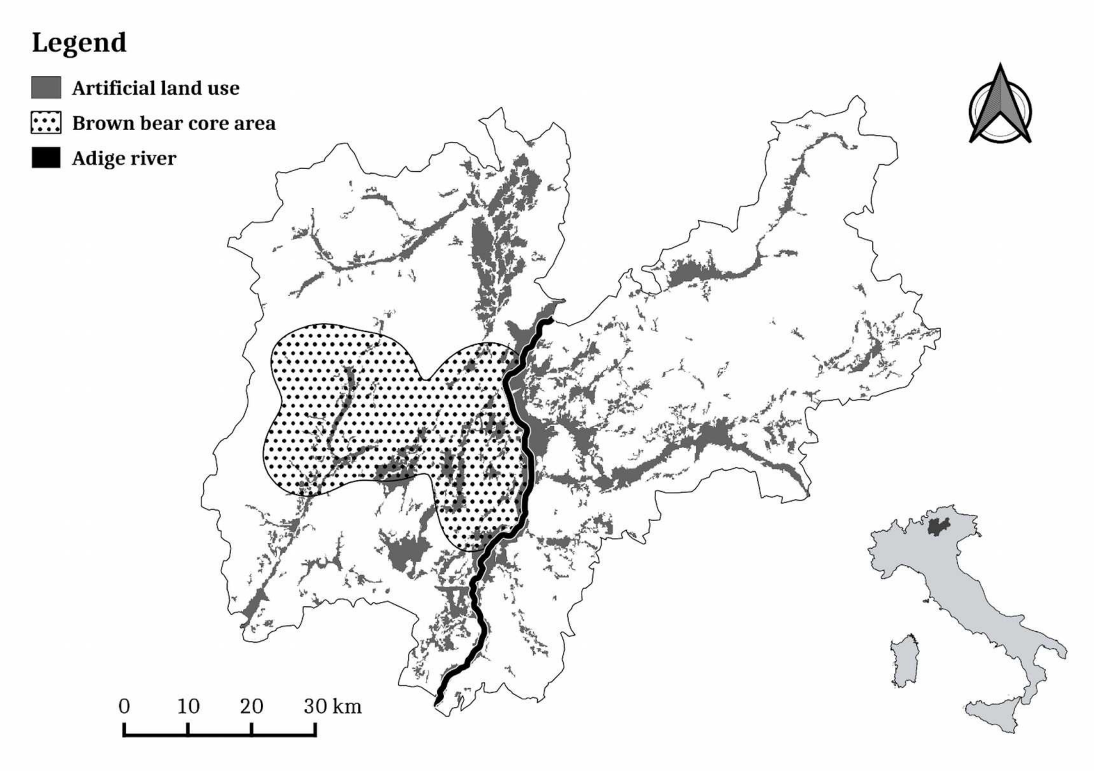

Figure 1 - Map of the study area and its location in the Italian Alps. In light gray, the distribution of artificial surfaces (i.e. altered by humans). In black the Adige river, which separates the region into two sectors: Western and Eastern Trentino. The dotted area indicates the brown bear population core areas as measured by the 95% Kernel Density Estimation of all GPS locations.

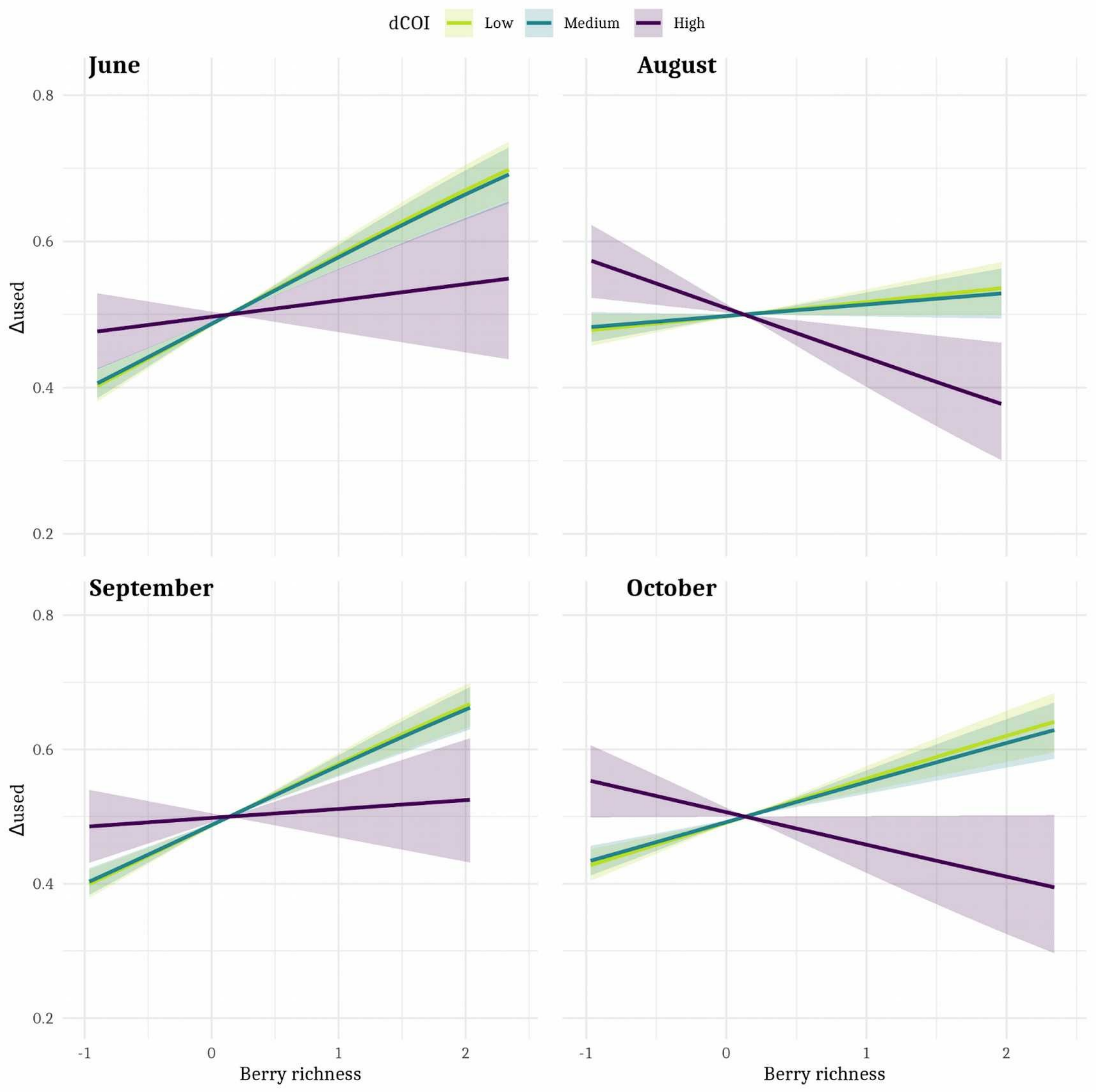

Figure 2 - Monthly plots with the relative change in the predicted probability of use (Δused) by bears at various level of berry richness (*r-berry*) relative to the average value (i.e., reference level, which corresponds to 0 because the explanatory variable is scaled). A negative change in the predicted probability of use indicates that bears are less likely to select that resource level than the average value. The predicted probability of use is 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.

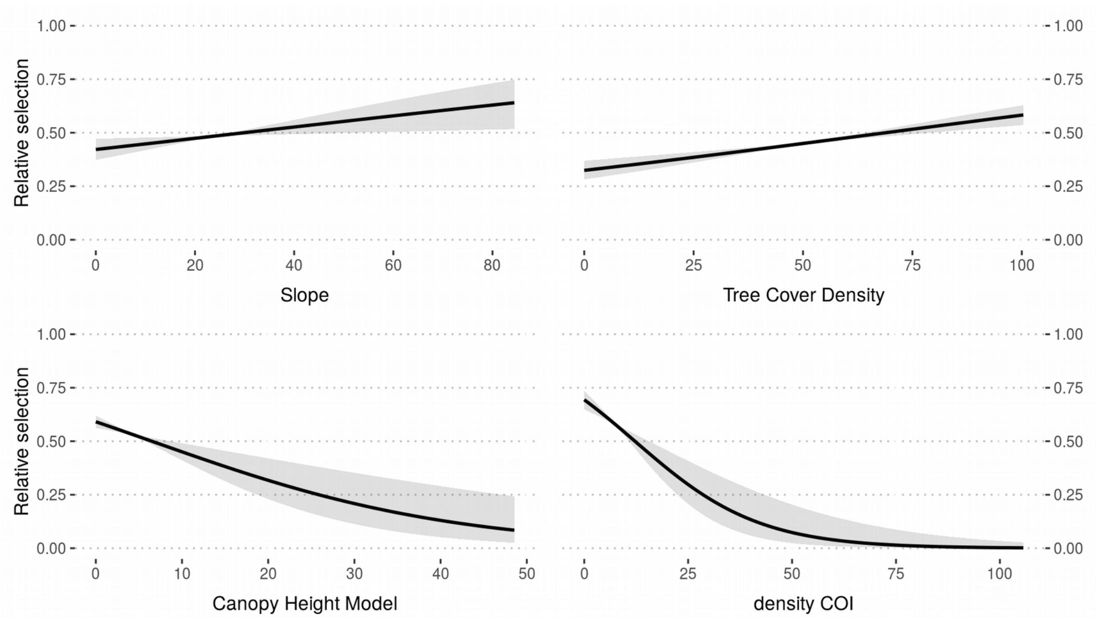

Figure 3 – Fitted regression lines with standard error showing the empirical association between resting site use and the significant environmental predictors, estimated using conditional logistic regression. The regression coefficients are derived from the best fitting model (i.e., with slope, tree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

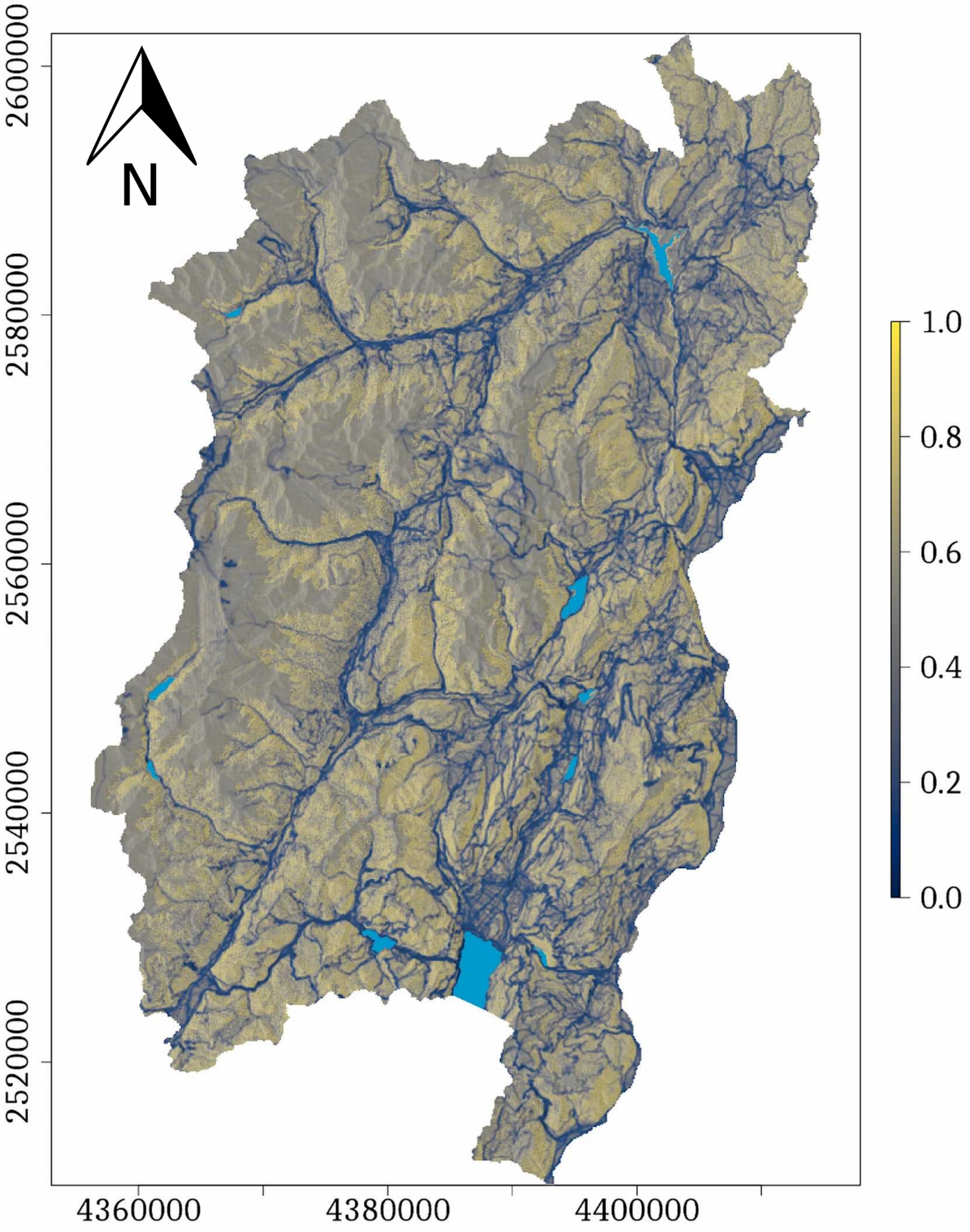

Figure 4 - Map of the predicted relative probability of use as resting location by brown bears in Western Trentino. The prediction is based on the estimated coefficient values from the mixed-effects conditional logistic regression model. As shown in the legend on the left, the level of predicted probability ranges from 0 (in blue) to 100 (in yellow). The map is in metric coordinates and has a resolution of 20 m pixel size.

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). For each monthly model, the explanatory variables, parameter estimates, 90% confidence intervals, and p-values are reported. At the bottom, the number of observations is reported (from a total of 21 animals/year).

	Dependent variable:					
	used					
	May	Jun	Jul	Aug	Sep	Oct
Slp	0.564***	0.456***	0.516***	0.446***	0.276***	0.357***
	(0.479, 0.649)	(0.365, 0.547)	(0.427, 0.605)	(0.368, 0.525)	(0.202, 0.351)	(0.276, 0.437)
Slp^2	−0.066*	−0.030	−0.153***	−0.148***	−0.013	−0.093**
	(−0.113, −0.019)	(−0.084, 0.023)	(−0.209, −0.097)	(−0.199, −0.098)	(−0.058, 0.031)	(−0.147, −0.040)
evi	0.625***	0.619***	0.975***	0.805***	0.528***	0.920***
	(0.545, 0.705)	(0.519, 0.719)	(0.876, 1.074)	(0.720, 0.889)	(0.454, 0.603)	(0.835, 1.004)
dCOI	−0.496***	−0.462***	−0.690***	−0.469***	−0.618***	−0.474***
	(−0.594, −0.397)	(−0.568, −0.357)	(−0.806, −0.575)	(−0.558, −0.380)	(−0.721, −0.514)	(−0.566, −0.382)
r-berry	0.125***	0.292***	0.137**	−0.028	0.266***	0.124**
	(0.064, 0.185)	(0.224, 0.361)	(0.065, 0.209)	(−0.090, 0.034)	(0.202, 0.331)	(0.057, 0.191)
dCOI:r-berry	0.017	−0.138*	−0.109	−0.166**	−0.159**	−0.218***
	(−0.070, 0.104)	(−0.229, −0.048)	(−0.216, −0.002)	(−0.251, −0.081)	(−0.254, −0.065)	(−0.308, −0.128)
Constant	−1.962***	−2.069***	−2.159***	−1.312*	−2.002***	−2.168***
	(−2.046, −1.879)	(−2.166, −1.972)	(−2.264, −2.054)	(−2.227, −0.396)	(−2.088, −1.916)	(−2.409, −1.927)
Observations	6,175	5,167	5,934	6,663	6,703	6,425
Note:						*p<0.05; **p<0.01; ***p<0.001

Table 2 - Results of the fitted mixed-effects conditional logistic regression used to assess brown bear selection of resting sites. The explanatory variables, parameter estimates (conditionally standardized), 90% confidence intervals, and p-values are reported.

Explanatory variable	Estimate	CI (90%)	p value
Slp	0.241	0.093 – 0.388	**<0.01**
Slp2	-0.067	-0.144 – 0.011	>0.05
TCD	0.412	0.271 – 0.554	**<0.001**
CHM	-0.308	-0.434 – -0.182	**<0.001**
dCOI	-0.752	-1.030 – -0.474	**<0.001**
r-berry	0.046	-0.097 – 0.188	>0.05
dCOI:r-berry	-0.016	-0.226 – 0.194	>0.05

Supplementary Material

S1. Animal capture details and protocols

In Italy, the brown bear is currently protected under European (Habitats Directive 92/43/EEC, incorporated in the Italian legislation via D.P.R. 357/97) and Italian Laws (L. 157/92), and included as a strictly protected species in the Bern Convention (1979). Under derogation of the aforementioned Habitat Directive, approved by the Italian Institute for Environmental Protection and Research (ISPRA), it is permitted to capture animals for research, public safety, and damage prevention purposes. Within these limits, all trapping and handling operations of wild brown bears are regulated by the "Interregional action plan for the conservation of the brown bear in the central-eastern Alps" (PACOBACE, 2010), approved by Directorial Decree n. 1810 of 5 November 2008 and amended by Directorial Decree Protocol 0015137 PNM of 30 July 2015.

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S2. Field validation of remotely identified resting sites

We visited as many clusters as possible between August and October 2018 and carried out field visits to verify the clustering technique used. We uploaded the centroids of the remotely identified clusters (Figure S2.1) into a handheld GPS device (Garmin GPS 64s) and visited a total of 96 hotspots over the reference period. At the specified locations, we looked for terrain depression or small portions of ground whose substratum may show signs of the bear's presence (e.g. Figure S2.2). In either case, we confirmed the presence of a resting site when 'hard facts' were found on the ground (i.e. hair, scat, or scratches). We found no clear signs of feeding or mating in the hotspot we visited. We could confirm the presence of a resting site 88% of the time. We were only able to confirm one 'bed' every hotspot identified. However, because we did not take into account the detectability of beds in the field (imposed by operators, the time of the year, or the substratum), it is reasonable to assume that the success rate could be higher than 88%. Overall, the remote detection of resting sites has proven effective, making the spatiotemporal clustering technique suitable for our research.

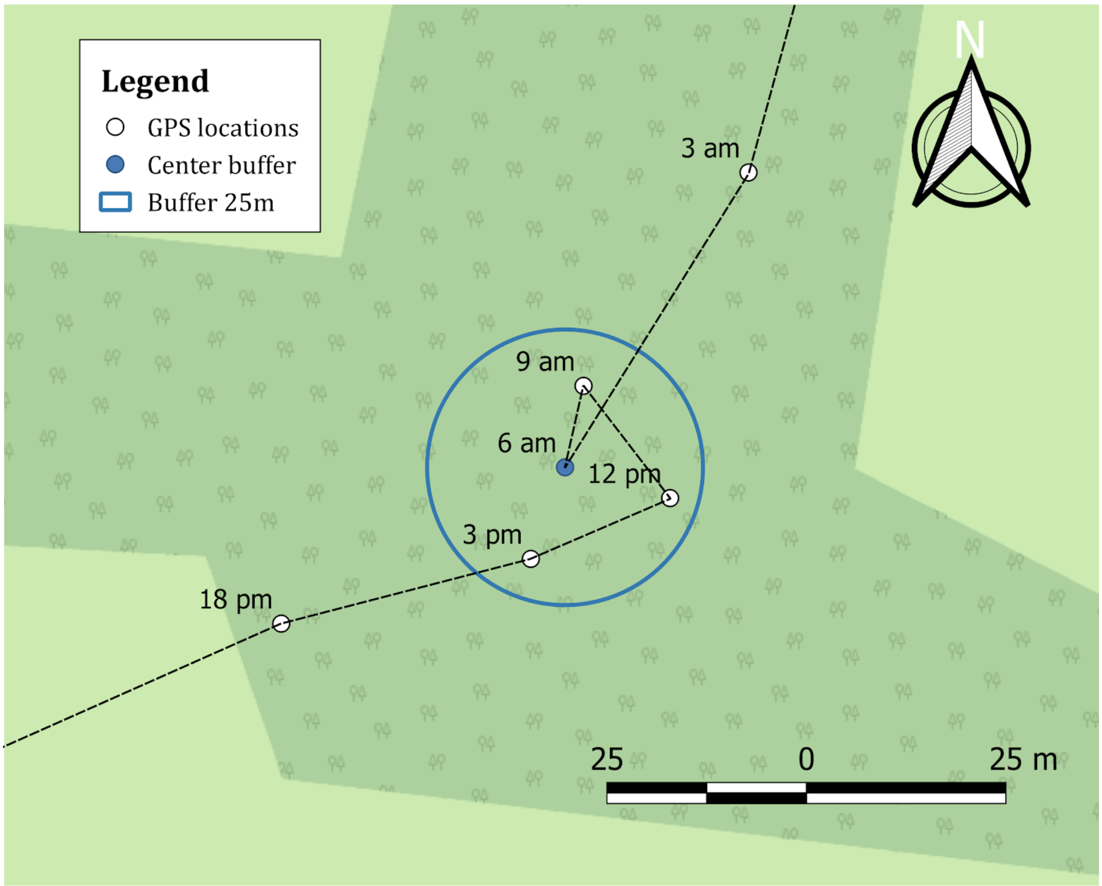


Figure S2.1 - Graphical representation of a cluster. Around each GPS location, a circle of 25 m radius is drawn and all the GPS locations within that circle counted. When a cluster contains locations for a period of time greater than 9 hours (as an example, the buffer drawn around the 6 a.m. location is shown in the figure), the cluster is classified as ‘bedsite’.

Figure S2.2 - Bear's resting site. The bed was identified via spatiotemporal clustering of GPS locations and confirmed by the presence of bear signs (hair, scat, or footprint). The aluminum bottle (1L) was placed in the center of the resting site as a reference scale.

S3. Description and correlation analysis of spatial covariates

We identified a set of topographic, resource, and anthropic disturbance variables as spatial predictors (Table S3.1) for the selection analysis. The acronym used in the analysis, the description, the unit, and the source are reported for each covariate. We used metric coordinates to facilitate the interpretation of the results, specifically, all the environmental layers were resampled to a common origin (ETRS89 / LAEA Europe Coordinate systems; EPSG: 3035) and resolution of 20 m (excluding the EVI at 250 m). We performed a correlation analysis between all variables and built models with covariates with $|r| \leq 0.6$ (Hinkle et al, 2003).

Table S3.1 - Selected spatial covariates measuring topography, resources, and human disturbance used in the analysis. For the full reference details, see Literature cited.

Covariate	**Description**	**Original Unit**	**Source**
Slp	Slope	Radians	LiDAR (Autonomous Province of Trento, 2008)
CHM	Canopy Height Model	Meters	LiDAR (Autonomous Province of Trento, 2008)
TCD	Tree Cover Density	Percentage	Copernicus Programme (Langanke et al, 2017)
EVI	Enhanced Vegetation Index	Index	MODIS (Vuolo et al, 2012)
r-berry	Monthly species richness of fruiting plants	Count	Tattoni et al (2019)
dCOI	Density of Cumulated Outdoor activity Index	Index	Corradini et al (2020)

Specifications on LiDAR

Between October 2006 and February 2008, the entire Autonomous Province of Trento was covered by two airborne LiDAR (Light Detection And Ranging) surveys. The first survey was conducted over the Adige valley using a TOPOSYS II laser scanner (TOPOSYS GmbH, Biberach, Germany) installed on a CASA C-212 Aviocar. The laser pulse wavelength and the pulse repetition frequencies were 0,4-0,8 nm and 100 kHz, respectively, with an average point density of at least 3.2 points/m^2 and a vertical error of 15/30 cm. The second survey was conducted over the rest of the Province using an OPTECH ALTM 3100C laser scanner (OPTECH, Toronto, Canada) installed on a Partenavia P.68 aircraft. The laser pulse wavelength and the pulse repetition frequencies were 1,56 nm and 85 kHz, respectively, with an average point density of at least 2.4 points/m^2 and a vertical error of 30/60 cm (Autonomous Province of Trento, 2008). The raw measurements were thus validated, filtered and processed, and the following products were released: (i) Digital Surface Model (DSM); (ii) Digital Terrain Model (DTM); (iii) Canopy Height Model (CHM). The rasters are provided at a resolution of 2 m, therefore for the analysis we have included the aggregated values (i.e. mean) for both slope and CHM.

Specifications on EVI

The Enhanced Vegetation Index (EVI), together with the best known Normalized Difference Vegetation Index (NDVI), is a vegetation index provided by NASA (Didan et al, 2015). It is an 'optimize' quantitative index of greenness which accounts for atmosphere influence and canopy background signal. EVI is computed as follow:

$$EVI = G \times \frac{(NIR - Red)}{(NIR + C_1 \times Red - C_2 \times Blue + L)}$$

where

- G is the Gain factor;
- NIR (Near-Infrared Region), Red, and Blue are atmospherically-corrected surface reflectance;
- C1 and C2 are coefficients of the aerosol resistance term;
- L is the adjustment that addresses non-linear spectral reflectance through canopy.

In the MODIS-EVI algorithm, the coefficients adopted are L=1, C_1=6, C_2=7.5, and G=2.5. Compared to the NDVI, the EVI is less sensitive to atmospheric-induced biases (by accounting for the blue band) while remaining sensitive to canopy variations without saturation in high biomass regions (Huete et al, 2002). Because of the linear relationship between the red-infrared ratio and the photosynthetically active radiation fraction (Running et al., 2004), the Vegetation Indexes are considered accurate indicators for large scale measurement of plant productivity. EVI is retrieved from daily, atmosphere-corrected, bidirectional surface reflectance derived by MODIS sensors on Terra and Aqua satellites. MODIS-specific compositing method assurance that low quality pixels are removed and 16-day composites are produced at a nominal spatial resolution of 250 m. We derived monthly smoothed EVI time series from the online platform hosted by BOKU Vienna (Vuolo et al, 2012).

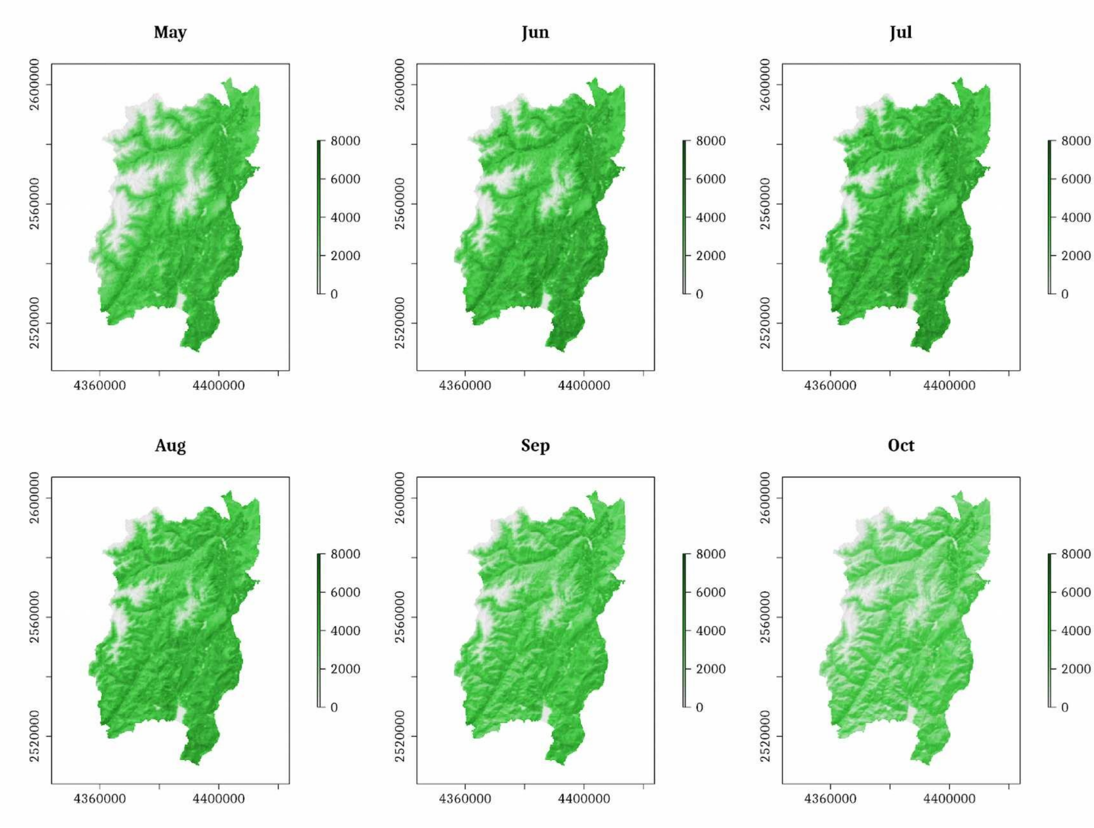
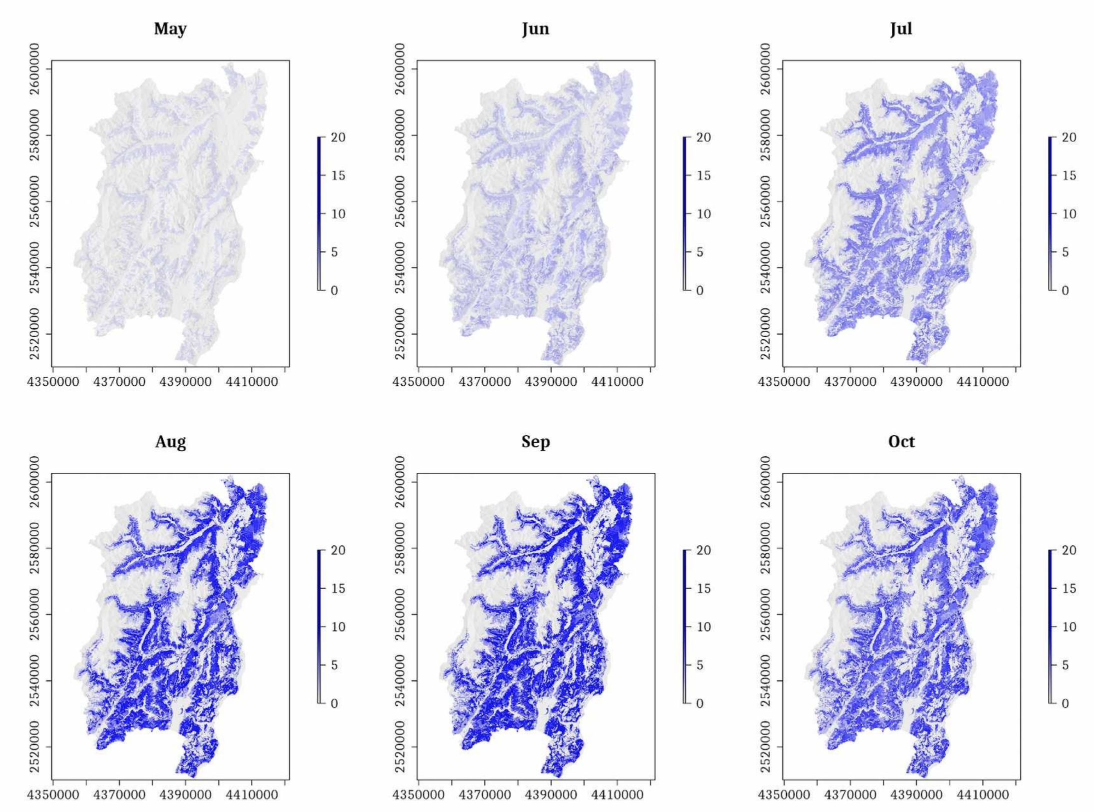


Figure S3.2 - Variation in the Enhanced Vegetation Index on a monthly basis over the study area.

Species richness of fruiting plants edible for the brown bear

We derived the fruit availability of 44 plant species commonly eaten or considered edible for the brown bears (Table S3.2) based on the GIS approach developed by Tattoni et al (2019). The proposed methodology combines spatial and non-spatial ecological information



id	Species name	Reference
1	*Amelanchier ovalis*	(Ciucci et al, 2014)
2	*Berberis vulgaris*	*edible for black bears* (Torgersen et al, 2001)
3	*Cornus mas*	(De Barba et al, 2014)
4	*Cornus sanguinea*	(Paralikidis et al, 2010)
5	*Cotoneaster nebrodensis*	*edible for humans* (Redžić & Ferrier 2014)
6	*Crataegus oxyacantha*	(Ciucci et al, 2014)
7	*Empetrum hermaphroditum*	(Hertel et al, 2016)
8	*Frangula alnus*	(Naves et al, 2006)
9	*Fragaria vesca*	(AA. VV. 2002)
10	*Hedera helix*	(Naves et al, 2006)
11	*Juniperus communis*	(Paralikidis et al, 2010)
12	*Juniperus nana*	(Paralikidis et al, 2010)
13	*Lonicera caerulea*	(Ripple et al, 2014)
14	*Prunus avium*	(Naves et al, 2006; Paralikidis et al, 2010; Ciucci et al, 2014)
15	*Prunus mahaleb*	(Ciucci et al, 2014)
16	*Prunus padus*	(Paralikidis et al, 2010)
17	*Prunus spinosa*	(Naves et al, 2006; Ciucci et al, 2014)
18	*Rhamnus catharticus*	(Ciucci et al, 2014)
19	*Rhamnus pumilus*	*possibly consumed* (Ciucci et al, 2014)
20	*Rhamnus saxatilis*	*possibly consumed* (Ciucci et al, 2014)
21	*Ribes petraeum*	*edible for humans* (Redžić & Ferrier 2014)
22	*Rosa arvensis*	(Ciucci et al, 2014)
23	*Rosa canina*	(Ciucci et al, 2014)
24	*Rosa corymbifera*	(Ciucci et al, 2014)
25	*Rosa pendulina*	(Ciucci et al, 2014)
26	*Rosa villosa*	(Ciucci et al, 2014)
27	*Rubus caesius*	(De Barba et al, 2014)
28	*Rubus canescens*	(Ciucci et al, 2014)
29	*Rubus hirtus*	(Ciucci et al, 2014)
30	*Rubus idaeus*	(De Barba et al, 2014)
31	*Rubus ser.*	(Ciucci et al, 2014)
32	*Rubus ulmifolius*	(Naves et al, 2006; Ciucci et al, 2014)
33	*Sambucus nigra*	*edible for black bears* (Mosnier et al, 2008)
34	*Sambucus racemosa*	(Fortin et al, 2013)
33	*Solanum dulcamara*	*edible for black bears* (Torgersen et al, 2001)
36	*Sorbus aria*	(Naves et al, 2006, Ciucci et al, 2014)

37	*Sorbus aucuparia*	(Naves et al, 2006, Paralikidis et al, 2010, Ciucci et al, 2014)
38	*Sorbus chamaemespilus*	*possibly consumed* (Ciucci et al, 2014)
39	*Sorbus torminalis*	(Naves et al, 2006)
40	*Vaccinium gaultherioides*	(Naves et al, 2006)
41	*Vaccinium myrtillus*	(Hertel et al, 2016)
42	*Vaccinium vitis-idaea*	(Hertel et al, 2016)
43	*Viburnum lantana*	(Naves et al, 2006)
44	*Viburnum opulus*	(Ogurtsov 2018)

Correlation matrices

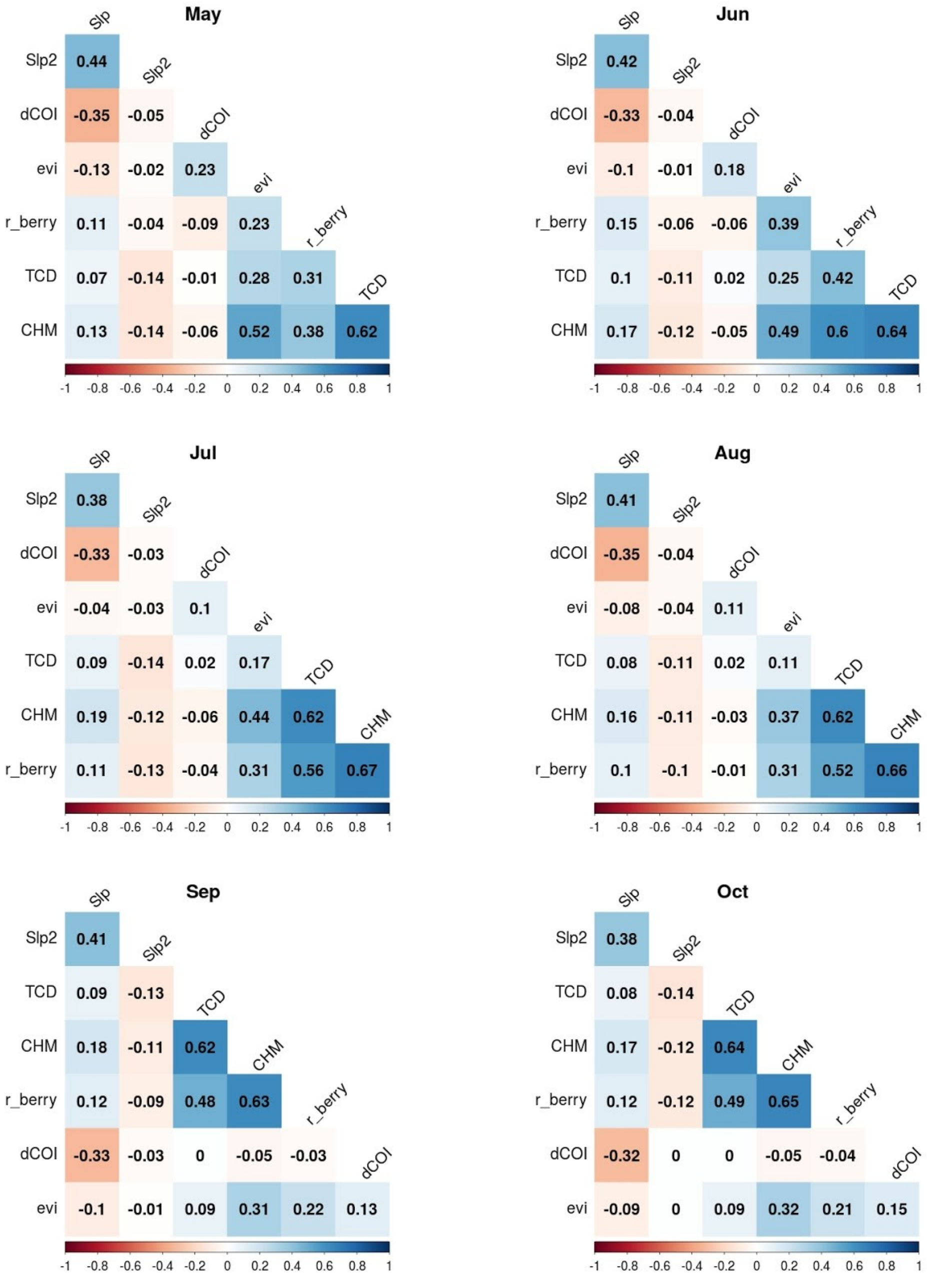


Figure S3.3 - Correlation matrix with the Pearson correlation coefficients between each variable chosen for the second-order habitat selection. Positive correlations are displayed in blue, while negative correlations in red. Color intensity is proportional to the correlation coefficient.

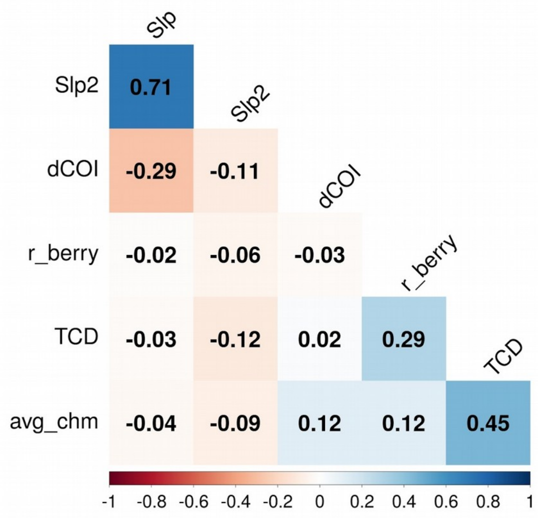


Figure S3.4 - Correlation matrix with the Pearson correlation coefficients between each variable chosen for the resting site selection. Positive correlations are displayed in blue, while negative correlations in red. Color intensity is proportional to the correlation coefficient.

Full reference details

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S4. Model comparison with ANOVA

Table S6.1 - Intra-monthly comparison of models via analysis of variance (ANOVA). For each month, we tested which combination of the terms dCOI and r-berry (interaction, additive, and both together ‘add_inter’) provided the best parsimonious fit of the data.

	Df	AIC	logLik	deviance	Chisq	Df.1	Pr(>Chisq)
May							
interaction	6	5183.311	-2585.656	5171.311			
additive	7	5073.912	-2529.956	5059.912	111.399	1	0.000
additive + interaction	8	5075.811	-2529.906	5059.811	0.101	1	0.751
Jun							
interaction	6	4256.301	-2122.151	4244.301			
additive	7	4124.739	-2055.370	4110.739	133.562	1	0.000
additive + interaction	8	4120.221	-2052.110	4104.221	6.519	1	0.011
Jul							
interaction	6	4789.446	-2388.723	4777.446			
additive	7	4628.378	-2307.189	4614.378	163.069	1	0.000
additive + interaction	8	4627.557	-2305.779	4611.557	2.820	1	0.093
Aug							
interaction	6	5568.419	-2778.209	5556.419			
additive	7	5487.712	-2736.856	5473.712	82.707	1	0.000
additive + interaction	8	5479.085	-2731.542	5463.085	10.628	1	0.001
Sep							
interaction	6	5755.461	-2871.730	5743.461			
additive	7	5558.271	-2772.135	5544.271	199.190	1	0.000
additive + interaction	8	5552.585	-2768.293	5536.585	7.685	1	0.006
Oct							
interaction	6	4991.180	-2489.590	4979.180			
additive	7	4898.515	-2442.258	4884.515	94.664	1	0.000
additive + interaction	8	4884.233	-2434.116	4868.233	16.282	1	0.000

Chapter 3

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

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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.

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 traveling 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 behaviors 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 hypothesized 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.

Materials and methods

Study area

The study was conducted in the province of Trento, 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).

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).

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).

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) standardized 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 ($b_{\text{All crossing}} = -0.59$, $p < 0.001$; $b_{\text{Low density}} = -1.13$, $p < 0.001$; $b_{\text{Medium density}} = -2.40$, $p < 0.001$; $b_{\text{High density}} = -2.24$, $p < 0.001$; 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; $b_{\text{Year(2020)}} = +1.33$, $p < 0.001$; 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 ($b_{\text{Year(2020)}} = 2.48$, $p < 0.001$; 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).

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).

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 behavioral 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. Importantly, this was not induced by higher availability of anthropogenic food, as the presence of attractants close to human settlements (e.g., garbage) were lower in 2020 than in previous years (Dolomiti Energia, 2021), hence excluding potential confounding effects.

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).

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 favoring 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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Tables and figures

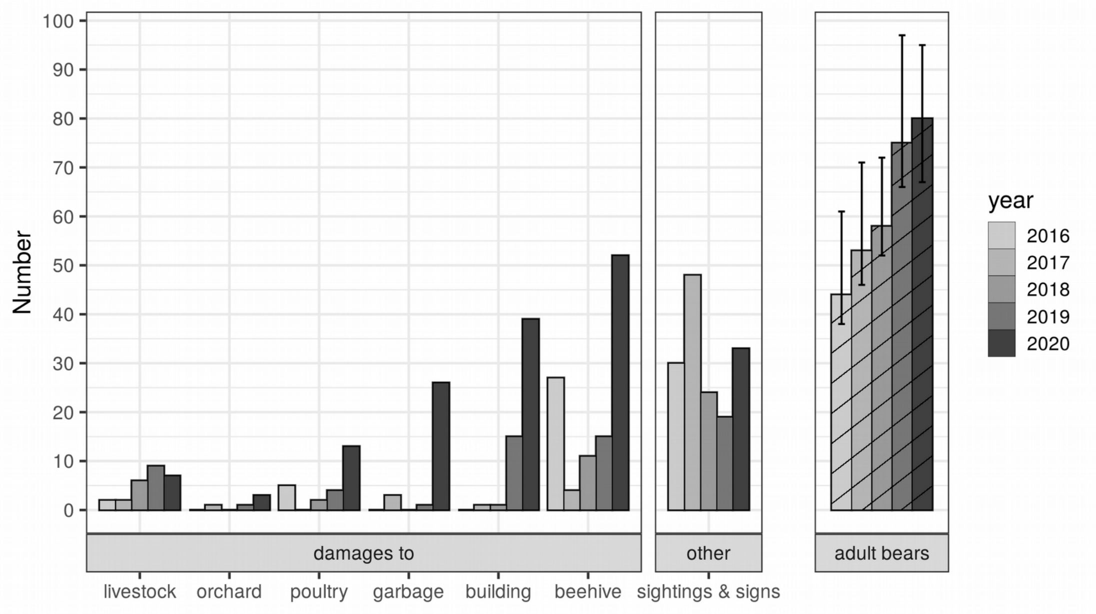

Figure 1 - Recorded occurrences (bear-related complaints classified by damage type, sightings, and signs of presence), during the period between March 9th and May 18th (time interval of the 2020 lockdown), in the years 2016-2020. Bars referring to successive years are colored in increasingly darker shades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

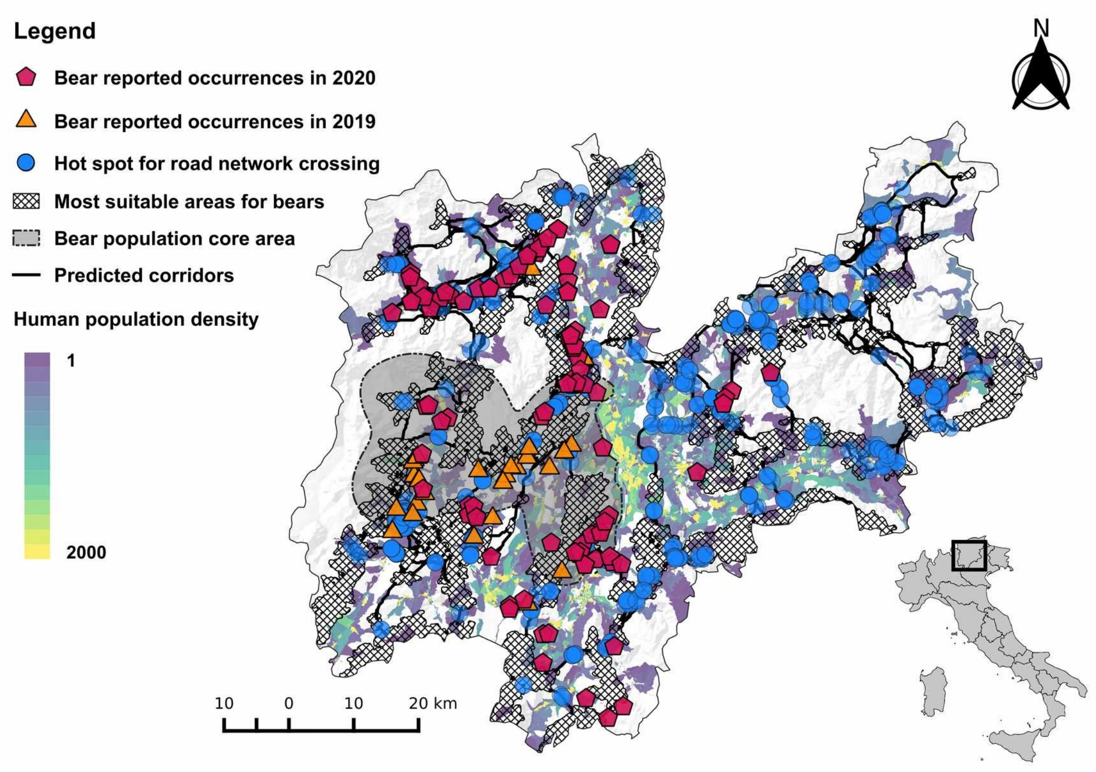

Figure 2 - Recorded bear occurrences (all event types, pentagon for 2020 and triangle for 2019) mapped over the province of Trento, Italy, during the lockdown period of March 9th to May 18th. The predicted most suitable bear habitat (cross-hatching) and relative corridors (continuous lines) identified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

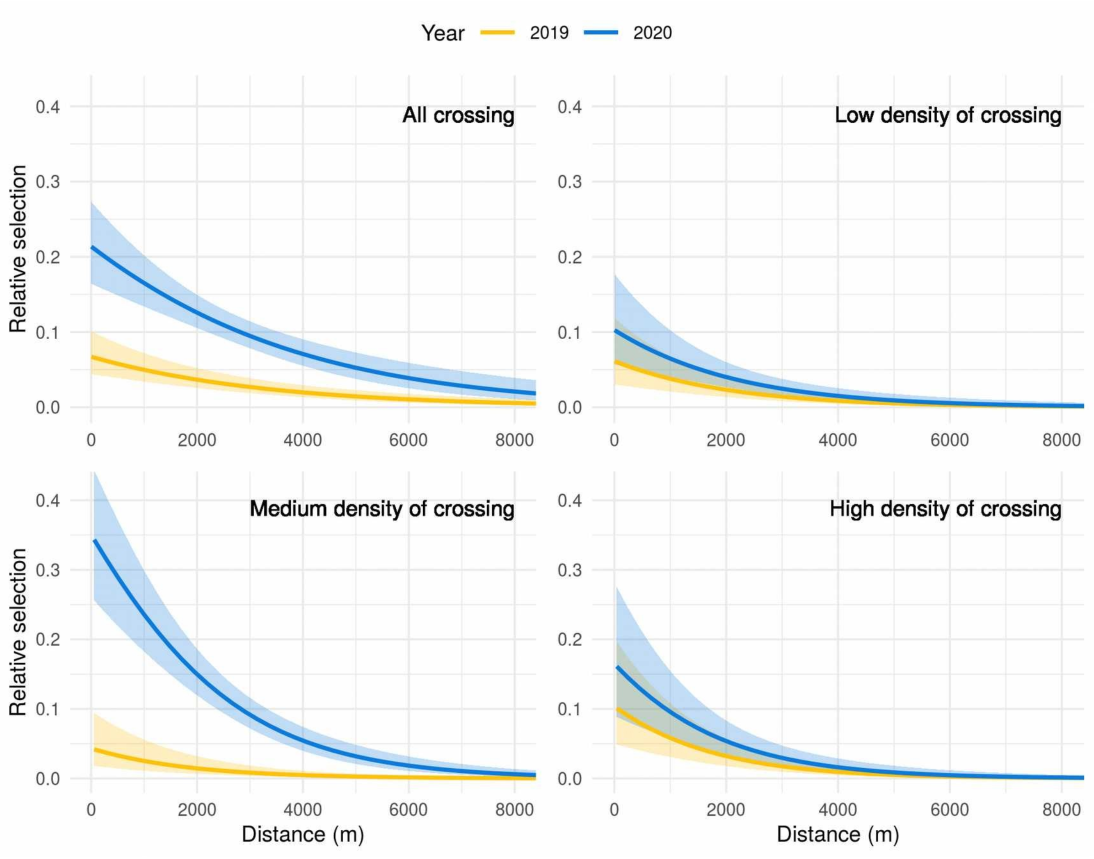

Figure 3 - Fitted regression lines with 95% confidence bands, estimated via Generalized Linear Models, of the empirical relationship between bear space use (as bear occurrences, compared to a random draw) and the proximity to hot spots for road network crossing (all, low -, medium -, and high density) 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.

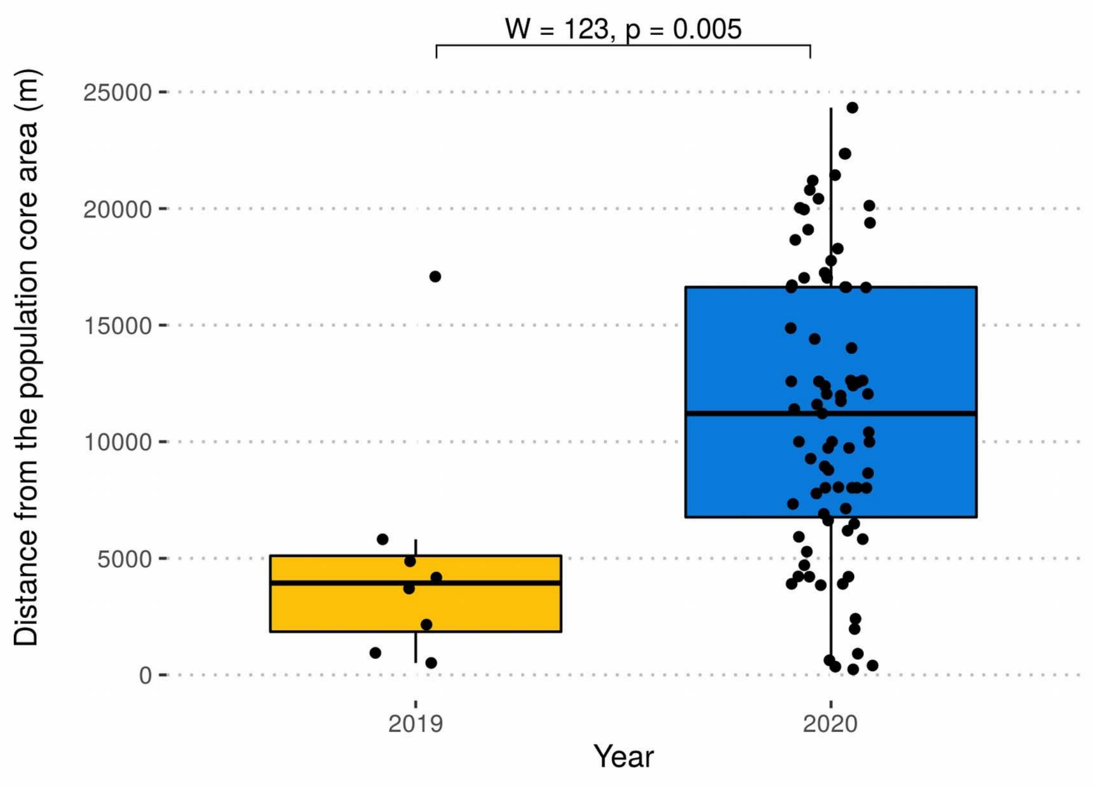

Figure 4 - Proximity of bear occurrences to brown bear population core area (Figure 2) in 2019 and 2020, reported during the period March 9th - May 18th. Each dot represents a bear occurrence reported with high spatial reliability (< 500 m accuracy). Above the boxplots: output of the two-sample Wilcoxon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

Table 1 - Results from the Generalized Linear Model with a Poisson error distribution fitted to the number of bear damage complaints, standardized 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

Supplementary Material

Table S1 - The type of damage caused by bears to each target, as well as the target's relative proximity to human dwelling.

Target	Type of damage reported	Proximity to human dwelling
Poultry	Fence damage, poultry slaughter	High
Garbage	Garbage pail damage, garbage consumption	High
*Building**	Damage to the structure, consumption of food supplies stored inside the building	Mixed
Beehive	Hive destruction, honey consumption, queen bee loss	Mixed
Livestock	Damage to the stable, animal slaughter (cattle, pigs, horses, dogs, or goats)	Low
Orchard	Fence damage, broken trees, fruit consumption	Low

* Mountain huts, farms, and houses

Table S2 - Selection coefficients from the most parsimonious generalized linear mixed model with a random intercept describing bear resource selection at the within home-range scale in the Autonomous Province of Trento, Italy (Peters, et al., 2015).

Covariates	**β-Coefficient**	**SE**	**p**
Elevation (100 m)	0.807	0.029	<0.001
Elevation2 (100 m)	-2.82e-04	9.58e-06	<0.001
North (aspect)	0.288	0.037	<0.001
Distance to bike trails (100 m)	0.047	0.003	<0.001
Distance to bike trails^2 (100 m)	-4.7e-06	2.63e-07	<0.001
Urban	-0.232	0.185	>0.05
Mixed	0.154	0.061	<0.05
Cultivated (without orchards)	-0.420	0.223	>0.05
Water	-0.696	0.246	<0.01
Shrub	0.392	0.056	<0.001
Model intercept	-6.225	0.509	<0.001

Source: *Peters, et al. (2015), Biol. Cons. 186, 123-133*

Table S3 - Number and type of bear-related complaints reported from March 9th to May 18th, in 2019 and 2020. For damages caused by bears, the specific targets are reported.

	Damages to						
	Beehive	**Garbage**	**Building**	**Livestock**	**Orchard**	**Poultry**	**Sightings & signs**
2016	27	0	0	2	0	5	30
2017	4	3	1	2	1	0	48
2018	11	0	1	6	0	2	24
2019	15	1	15 *	9	1	4	19
2020	52	26	39 **	7	3	13	33

Note: * 5 mountain huts, 8 farms, 2 houses; ** 32 mountain huts, 7 farms, 3 houses;

Table S4 - Complete model outputs from Generalized Linear Models with a Poisson error distribution fitted to the occurrence of bear-related complaints in dependence on the type of complaint and year of occurrence. The estimated coefficient values (b), the standard error, and the P-values (*p<0.05; **p<0.01; ***p<0.001) are reported for each covariate. When estimated coefficients are absent, no records were available for that year.

	Damage type						
Year	**Livestock**	**Orchard**	**Poultry**	**Garbage**	**Building**	**Beehive**	**No. bears**
2016	-0.560 (0.627)	-	-0.368 (0.434)	-	-	-0.059 (0.199)	-0.598 ** (0.188)
2017	-0.847 (0.690)	-0.405 (0.913)	-	-1.649 *** (0.488)	-2.970 *** (0.725)	-2.159 *** (0.431)	-0.412 * (0.177)
2018	0.134 (0.518)	-	-1.466 * (0.641)	-	-3.664 *** (1.013)	-1.243 *** (0.293)	-0.322 (0.172)
2019	0.357 (0.493)	-1.099 (1.155)	-1.179 * (0.572)	- 3.258 ** (1.019)	-0.891 ** (0.297)	-1.179 *** (0.286)	-0.065 (0.161)

Table S5 - Intra-model comparison via analysis of variance (ANOVA) for each of the fitted Generalized Linear Models for prediction (ii). For each model evaluating the proximity of bear occurrences to different types of hot spots for road network crossing, we tested which combination of terms provided the best parsimonious fit of the data.

	Terms	Deviance	Resid. Dev	Pr(>Chi)
All crossings	~ 1		1055.88	
	Year	48.95	1006.93	<0.001
	Distance	37.39	969.53	<0.001
	Year:Distance	0.15	969.38	>0.05
Low density of crossings	~ 1		361.90	
	Year	2.76	359.13	>0.05
	Distance	30.92	328.21	<0.001
	Year:Distance	0.30	327.91	>0.05
Medium density of crossings	~ 1		665.10	
	Year	63.73	601.37	<0.001
	Distance	105.62	495.74	<0.001
	Year:Distance	0.01	495.73	>0.05
High density of crossings	~ 1		312.43	
	Year	2.13	310.30	>0.05
	Distance	55.08	255.22	<0.001
	Year:Distance	0.04	255.18	>0.05

Table S6 - Model selection results for models testing the proximity of bear occurrences to different types of hot spots for road network crossings, used to test prediction (ii). The explanatory variables, degree of freedom, second-order Akaike Information Criterion (AICc) scores, and delta AICc (ΔAICc) are reported for each model. Models are ranked by AICc scores for each type of road network crossing.

	Model	**df**	**AICc**	**ΔAIC**
All crossings	Distance + Year	3	975.54	0
	Distance + Year + Year:Distance	4	977.40	+1.86
	Year	2	1010.93	+35.39
	Distance	2	1021.21	+45.67
	~1	1	1057.88	+82.34
Low density of crossings	Distance + Year	3	334.23	0
	Distance	2	334.85	+0.62
	Distance + Year + Year:Distance	4	335.93	+1.70
	Year	2	363.14	+28.91
	~1	1	363.90	+29.67
Medium density of crossings	Distance + Year	3	501.76	0
	Distance + Year + Year:Distance	4	503.75	+1.99
	Distance	2	559.95	+58.19
	Year	2	605.37	+103.61
	~1	1	667.10	+165.34
High density of crossings	Distance	2	261.20	0
	Distance + Year	3	261.23	+0.03
	Distance + Year + Year:Distance	4	263.20	+2.00
	Year	2	314.31	+53.11
	~1	1	314.43	+53.23

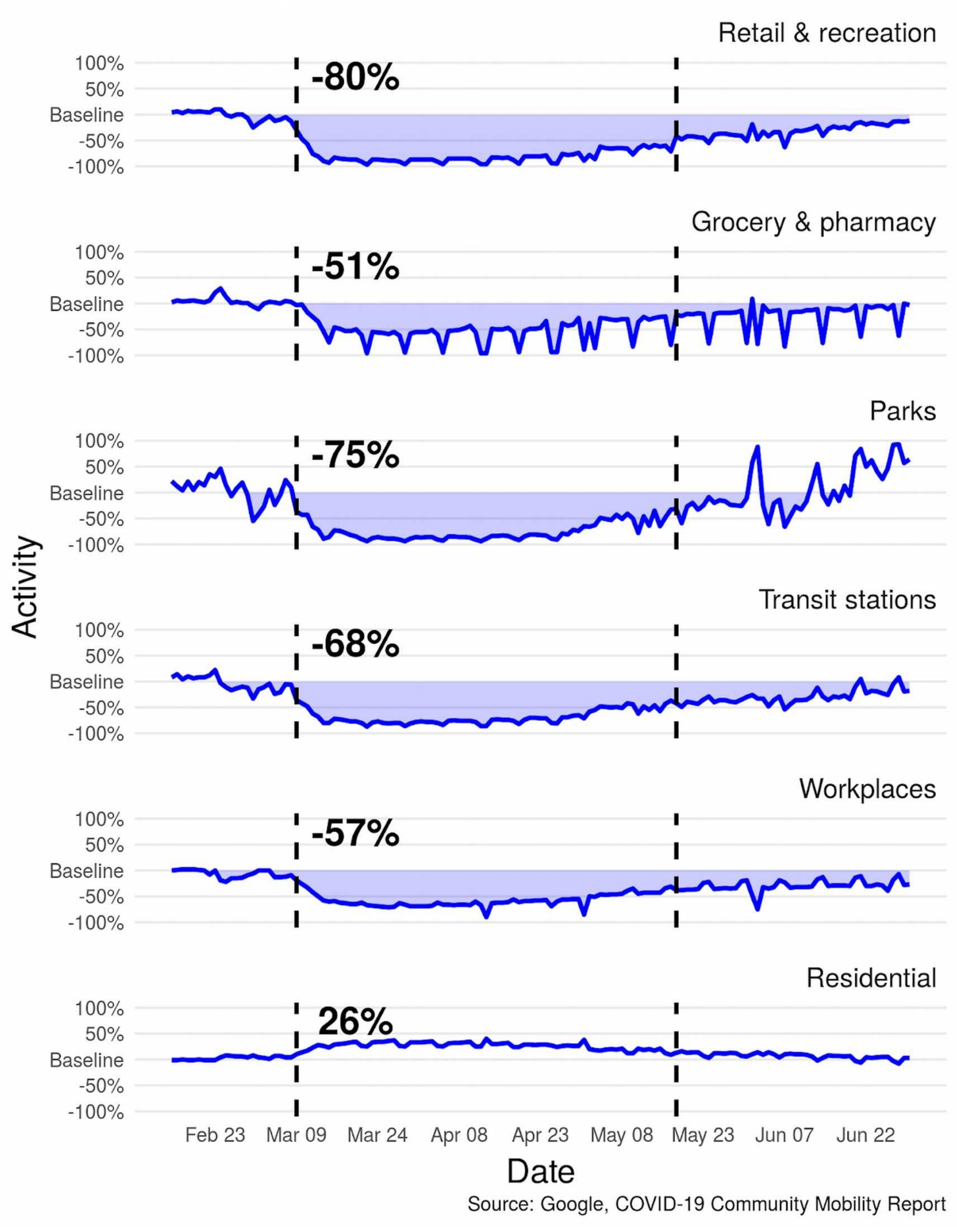

Figure S1 - Mobility changes in the Province of Trento by locations, based on aggregated and anonymized data (Google, 2021). The baseline is the median value, for the corresponding day of the week, during the period Jan 3–Feb 6, 2020. The dashed lines represent the beginning (March 9th) and the end (May 18th) of the 2020 lockdown. The difference in movement between the baseline and the lockdown is reported as a percentage difference.

Figure S2 - Some examples of bear-related damages and occurrences. Clockwise from top-left: Damaged mountain hut door (L. Pincigher - Archivio Servizio Faunistico PAT), damaged beehives (R. Bernardi - Archivio Servizio Faunistico PAT), toppled garbage bin (M. Zeni - Archivio Servizio Faunistico PAT), and bear front and rear footprints (G. Rastrelli).

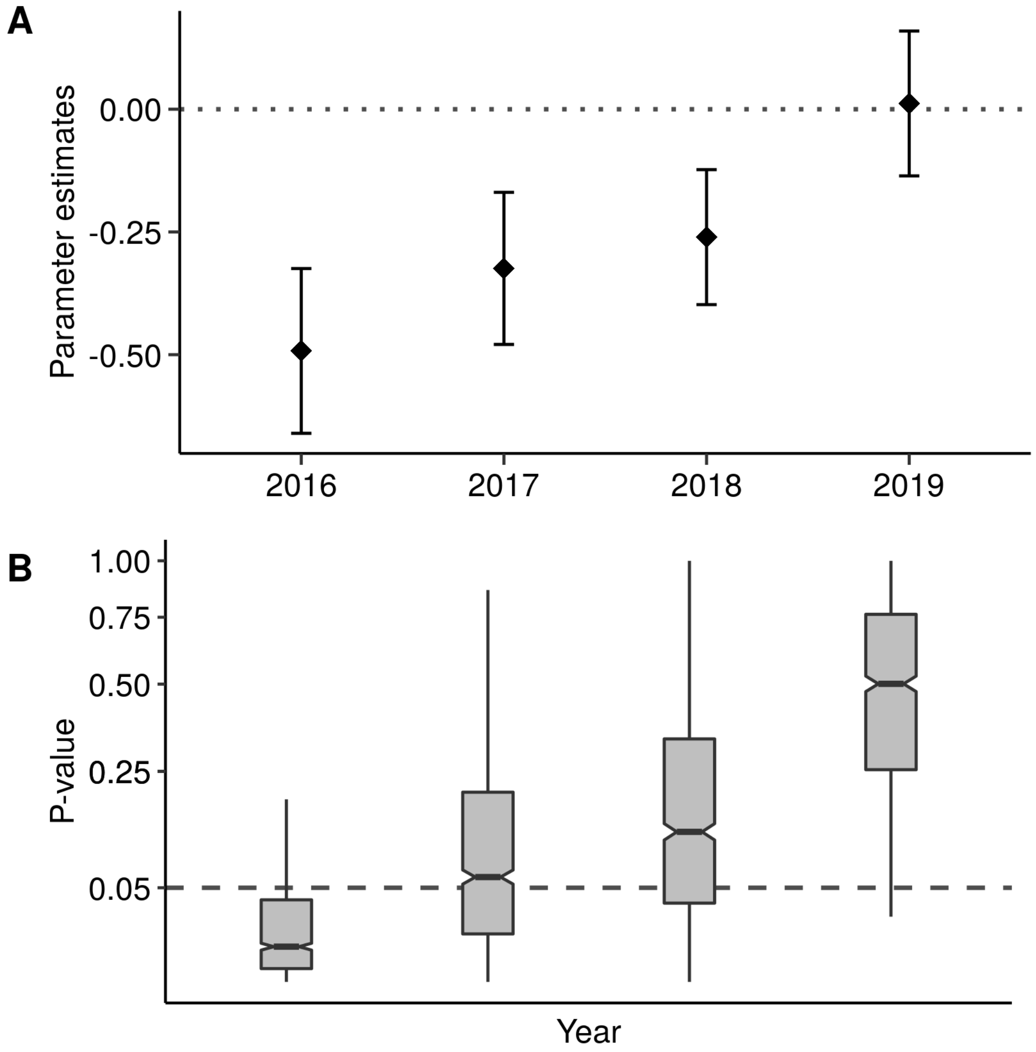

Figure S3 - A: Bootstrapped regression coefficients (mean ± 1 SD) of the fitted GLM for testing the increase in abundance between 2020 and any other year (2016-2019). B: P-value distributions of bootstrapped model's parameters. The dashed line marks the statistical significance level ($p = 0.05$) and the boxplot notch the 95% confidence interval of the median. The y-axis is scaled (by square root transformation) to highlight the values near the reference significance level.

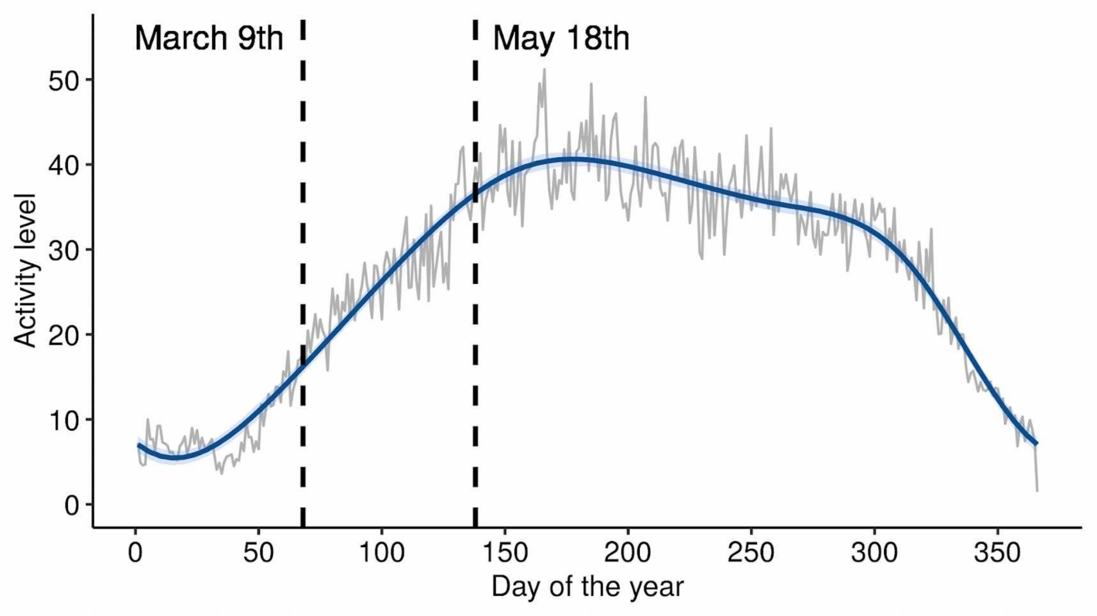

Figure S4 - Average daily activity pattern of brown bears in the Central Alps. Individual forward-backwards movement (i.e., +-2G, scaled from 0 to 255) computed using a tri-axial accelerometer (4 Hz) from Vectronic GPS collars is used to determine the average activity level. We used activity data of animals collared between 2006 and 2019 (8 females, 4 males), for a total of 25 animal/year. The dashed lines represent the beginning (March 9th) and the end (May 18th) of the 2020 lockdown.

Chapter 4

Density-dependence effects on the body composition of a large opportunistic omnivore

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Abstract

Animal population growth is influenced by density-dependent factors. Individual performance and local density are intrinsically linked through a feedback mechanism that lead to population-level changes; yet, density-dependent processes are normally examined at the population level, making rapid demographic change assessment difficult. In a rapidly changing world, it is thus critical to identify and understand such regulatory processes early on to gain a better understanding of the evolution of life history traits and, ultimately, population persistence in the environment. This is especially significant for long-lived omnivores, whose persistence is critical to the ecosystem's function, but whose slow life histories make them susceptible to abrupt changes. In this study, we investigated whether density-dependent factors drove changes in lean body mass and fat percentage, both indicators of individual performance, in one of the world's largest terrestrial omnivores, the grizzly bear. We examined four main hypotheses using longitudinal morphometric data from 418 grizzly bears captured for scientific purposes between 2000 and 2020 in the Greater Yellowstone Ecosystem. While controlling for external factors such as management practices and land ownership, individual lean body mass was found to be negatively related to population density, especially among females and individuals in the growth phase. The Greater Yellowstone Ecosystem has been subjected to significant landscape-level perturbations during the last two decades, combined with steady local bear population density increase. When controlling for recent high-calorie food perturbations, our findings revealed that grizzly bear body fat levels or accumulation over this time period was not affected by population density. As opportunistic large omnivores, grizzly bears most likely modified their feeding tactic and morphologically adapted in the face of increased interference competition. In a changing world where environmental perturbations, particularly those caused by humans, are increasing in frequency, it will be critical to disentangle the mechanisms that drive population dynamics, both for species persistence and for the health of entire ecosystems.

Keywords: Eco-evolutionary dynamics; omnivory; density-dependence; ecosystem perturbations; Greater Yellowstone Ecosystem; *Ursus arctos;*

Introduction

Body mass and body composition (fat vs. lean mass) are indicators of performance directly related to fitness of mammals: larger or fatter individuals usually have a higher probability of survival and a greater capacity to invest energy in reproduction (Stearns, 1992; Stephens, et al., 2009; Wilder et al., 2016), thus increasing their reproductive success. This particularly applies to long-lived mammal species that rely on energy accumulation for long-term survival and reproductive strategies (Oftedal, 2000). When population density of long-lived mammals increases toward maximal levels in a system (i.e., carrying capacity; Stephens et al., 2019), a sequence of changes in vital rates has been postulated to occur. First, the mortality rate of immature animals increases, followed by an increase in age of first reproduction (i.e., primiparous females), a reduction in the reproductive rate of adult females and, lastly, an increase in the mortality rate of adults (Eberhardt, 2002). In large mammals, because females are predominantly responsible for parental care, the first vital rate that generally changes with population density (i.e., juvenile survival) is directly related to maternal body mass (e.g., Gaillard et al., 1997) and body composition (e.g., Robbins et al., 2012). Alternatively, when population density is high, fertile females may not reproduce due to the high competition for resources to be allocated to embryo development (i.e., insufficient body fat to sustain the pregnancy; Robbins et al., 2012) or offspring care, resulting in reproductive suppression (Wolff, 1997). Although female performance can be a reliable indicator of changing population density, quantifying variations in vital rates of long-lived mammalian populations can take decades (Western, 1979), potentially limiting the ability to detect the emergence of density-dependent effects.

Individual performance and population density are intrinsically linked through a feedback mechanism: in order to grow larger and thus enhance fitness, individuals must acquire proportionally more resources, the availability of which often decreases as density increases (i.e., intraspecific competition; Chesson, 2000). The importance of density dependence in influencing demographic processes of populations is well established (Reznick et al., 2002), particularly in isolated populations with no immigration and emigration (Hixon et al., 2002). Density-independent factors, such as landscape perturbations or extreme weather, may affect these mechanism by lowering carrying capacity due to variation in resource availability (Skogland, 1985; Woodworth-Jefcoats et al., 2017), which can amplify the impact of high densities on life-history traits (Fowler, 1981). In the face of competition or perturbations, animals may adopt different behavioral, reproductive, or feeding tactics to maintain high individual performance (Kruuk and Parish, 1982;

Pettorelli et al., 2005; Taylor and Norris, 2007; Fattebert, et al., 2019). However, rapid environmental changes, such as those induced by humans, may create mismatching conditions for species that cannot adapt quickly (Sih et al., 2010). Long-lived animals, because of their slow life history, might not be able to adapt fast enough to maintain individual performance. Climate change, for example, may either directly affect individual performance in large mammals with increasing temperature altering the thermal balance (Fuller et al., 2016; Semenzato et al., 2021), or indirectly by shifting the spatio-temporal distribution of resources (Pettorelli et al., 2007). Droughts and shifts in resource waves in particular can disrupt animals' ability to track resources (Aikens et al., 2020) and directly affect fat accumulation and thus timing of birth (e.g., migratory ungulates; Aikens et al., 2021).

The adaptive capacity to respond to spatio-temporal environmental changes varies substantially among species. Clavel et al (2011), for example, observed that generalist species are outperforming and gradually replacing specialist species globally because of their plasticity in responding to climate and land use change. Omnivory, a common trait among generalist species, may be a beneficial strategy in a changing environment because it enables animals to shift their diet when a resource becomes temporarily depleted, allowing recovery of the resource and ultimately stabilizing the system (Kratina et al., 2012). Whereas environmental stochasticity affects population density over time (Sæther, 1997), which in turn influences life-history traits in large mammals, omnivores, unlike specialist species (e.g., herbivores; Bårdsen and Tveraa, 2012), may be able to buffer short-term variations in habitat productivity. For instance, omnivores require smaller home ranges than carnivores with comparable body size in environments with low productivity (Hirt et al., 2021), indicating greater capacity per unit area to obtain energy. Although generalist species may have an evolutionary advantage compared with specialists in responding to changes in the environment, they will eventually be affected by increased population density and competition for limited resources. This has been observed in medium-bodied omnivores whose demographics are influenced by other factors such as group size or territoriality (e.g. badger, Kruuk and Parish, 1982; kit fox: Dennis and Otten, 2000), but few studies, to our knowledge, have disentangled the effects of population density and environmental alterations on individual performance of solitary, non-territorial large-bodied omnivores. By examining variation in body mass and composition among individuals across a range of local population densities, we can gain important insights into the population dynamics of large-bodied omnivores. Furthermore, by partitioning body composition, we can evaluate the impact of past conditions, as reflected by lean body mass, and current conditions,as expressed by percentage body fat, that individuals were exposed to.

The Greater Yellowstone Ecosystem (GYE), which is home to most of North America's large mammal species, is no exception to environmental fluctuations. Despite being one of the world's largest nearly intact temperate ecosystems, environmental changes have occurred in recent decades (Gibson 2007; Gude et al., 2007; Romme et al., 2016). Within the large mammal community, the brown bear (*Ursus arctos*), commonly referred to as grizzly bear in the interior range of North America, has received particular attention for over 60 years. They have not been subjected to regulated hunting since 1975, the year of its listing under the U.S. Endangered Species Act and their diet consist primarily of natural foods following the closure of municipal garbage dumps in 1968–1979 (Haroldson et al., 2008; Gunther et al., 2014). One of the world’s largest terrestrial omnivores, grizzly bears consume food resources across multiple trophic levels depending on availability (Gunther et al., 2014). Omnivory in grizzly bears is a functional adaptation, allowing them to live in a broad range of environments (i.e., Holarctic distribution; McLellan et al., 2017) and exploit variation in the nutritional composition of food sources (Coogan et al., 2018). Besides their opportunistic feeding strategy, grizzly bears are long-lived (>25 yrs), and are thus exposed to habitat variability and competition over many years. They are also non-territorial and can track resources over extensive areas, and have no natural predators except for conspecifics. An important aspect of their life history strategy is the need to acquire sufficient stored energy reserves during their active months to support a 3- to 7-month denning period during hibernation. For reproductive-age females, stored energy must also be adequate to support pregnancy and lactation while denned (> 20% body fat ; Robbins et al., 2012). Consequently, grizzly bear body mass varies considerably within their annual cycle, from lows in early to mid-summer, reflective of lean body mass, to substantial mass gain prior to denning and onset of hibernation. Additionally, because grizzly bears grow rapidly during their first years of life and subsequently plateau at a certain age (i.e., growth asymptote; Bartareau et al., 2011), age-related changes in body mass are particularly significant during the early life cycle stage.

The conservation status of the Yellowstone grizzly bear population improved in response to concerted management efforts beginning in the early 1980s and was driven by relatively high survival rates for several decades (Schwartz et al., 2006). Population growth has slowed since the early 2000s, primarily due to lower rates of immature survival and lower reproductive transition probability for females in presence of density dependence (van Manen et al., 2016). However, it remains uncertain to what extent intraspecific competition (i.e., density-dependent factors) influence individual performances such as sex-specific growth and body composition (van Manen et al., 2016). This is a particularly relevant question given environmental perturbations (i.e., density-independent factors) involving several high-calorie food sources in recent decades (e.g., Macfarlane et al., 2013; Haroldson et al., 2005). Using two decades of body composition estimates (lean body mass and percentage body fat) for grizzly bears captured in the GYE, we tested research hypotheses associated with grizzly bear population density variation on individual level performance (Table 1), while controlling for exposure to environmental changes. We first hypothesized that variation in lean body mass of grizzly bears across the GYE from 2000 to 2020 was linked to that of local population density, particularly before bears reached their age-dependent asymptotic body mass. Similarly, we hypothesized that, given the bear's ecological plasticity, body composition (i.e., fat percentage) would decline with greater local population density, particularly for growing individuals, and would remain constant across decades characterized by substantial changes in availability of food resources. We tested four hypotheses by assessing the following predictions: (i) lean body mass of bears is negatively related to grizzly bear local population density, (ii) lean body mass of growing individuals, more so than mature individuals, is negatively related to local population density, (iii) body fat percentage is negatively related to grizzly bear population density, irrespectively of food resource variation through decades and (iv) this relationship is evident among growing individuals more so than mature individuals. Alternatively, because body fat is essential for grizzly bear hibernation and, more specifically, for female reproduction and offspring care, bears may prioritize fat storage over lean body mass when allocating energy from food consumption. Accordingly, reduced access to foods, caused by increasing interference competition, should primarily result in reduction in lean body mass. We thus predict that body fat levels among individuals do not decrease as population density increases, but lean body mass does.

Materials and methods

We tested our research hypotheses by examining factors that may influence individual variation in lean body mass and body fat in Yellowstone grizzly bears. We estimated sex-specific lean body mass growth using von Bertalanffy growth curves. We then examined if individual variation in lean body mass for two life stages was associated with a spatially explicit covariate of local population density (H1 and H2). Because of different land ownership and management practices (Figure S1), the history of population dynamic processes varies within the study area: Yellowstone National Park is the core protected area where grizzly bears have always been present, whereas densities increased in adjacent areas starting in the 1990s and 2000s and outlying areas of the ecosystem were re-occupied only in the last decade. Therefore, we controlled for spatial heterogeneity of population dynamic histories as described under covariates. We used measurements from the beginning of the fat accumulation phase to the onset of hibernation to estimate the effect of population density and life stage on body composition, while controlling for decadal variation in food resource availability from the 2000s to 2010s (H3 and H4).

Study area

The study area consisted of occupied grizzly bear range in the GYE (68,736 km2 in 2018) and included Yellowstone and Grand Teton National Parks, portions of 5 adjacent national forests, and state and private lands in Wyoming, Montana, and Idaho. The GYE consists of a high-elevation plateau surrounded by 14 mountain ranges with elevations greater than 2,130 m, and contains the headwaters of 3 continental-scale rivers. Summers are short and most average annual precipitation (50.8 cm) falls as snow. Vegetation transitions from low-elevation grasslands through conifer forests at mid-elevations, reaching alpine tundra around 2,900 m.

Capture and handling

Grizzly bears were captured during 1975–2020 as part of a long-term monitoring program. Captures were conducted under U.S. Fish and Wildlife Service Endangered Species Permit [Section (i) C and D of the grizzly bear 4(d) rule, 50 CFR17.40(b)], with additional permits from the National Park Service, and state wildlife agencies of Wyoming, Montana, and Idaho. Capture and handling conformed to the Animal Welfare Act and to U.S. Government principles for the use and care of vertebrate animals used in testing, research, and training (U.S. Geological Survey ACUC no. 2021.1). We captured bears in frontcountry (road access) and backcountry (no road access) settings to obtain a geographically representative sample of the population. Specifically, grizzly bear captures were conducted with the aim of obtaining adequate coverage across the distribution of bears at the time of sampling, as well as a representative sample by age, sex, age class, and considering other covariates that influence demographics. A more detailed description of the sample's geographic distribution and randomness is described elsewhere (Schwartz et al., 2006).

Morphometric measurements

As part of a suite of morphometric measurements, we obtained body mass using an electronic scale (Artech Model 20210-2K s-beam load cell, Artech Industries Inc., Riverside, CA and a 4406 indicator A&D Co., Ltd. Tokyo, Japan) and estimated body fat percentage with Bioelectrical Impedance Analysis (BIA; Quantum II, RJL Systems, Clinton Township, MI). We calculated lean body mass (kg) by subtracting body fat mass from total body mass. We extracted a vestigial, first premolar tooth for age estimation based on cementum annuli, which was conducted by Matson's Laboratory (Manhattan, MT) (Matson et al., 1993).

Analysis

Determining lean body mass and growth

Grizzly bears accumulate fat reserves over the course of the active season (April–November) in preparation for hibernation, which can cause substantial seasonal influence on body mass. Consequently, we focused on lean body mass for our analysis of growth because it is seasonally invariant. We tested this assumption by calculating the Kendall rank correlation coefficient between lean body mass of mature bears and the central months of the active season (May–October). Mature bears were defined as bears who have reached 95% of their sex-specific asymptotic lean body mass (as defined by von Bertalanffy growth, see below).
We excluded bears from our analysis that were captured for conflict management purposes, individuals whose age was not estimated via cementum annuli, measurements from same-year recaptures, and any values identified as statistical outliers for which we had evidence of measurement or transcribing errors. We used lean body mass of bears of all ages to estimate growth, but we excluded dependent-age (<2 yrs) individuals to estimate body fat gain. Because proximity to carcass redistribution sites used for deposition of road-killed ungulates was positively correlated with lean body mass in some males (see Supporting Information S2), we also excluded 52 male grizzly bears captured in proximity (<2,000 m) of such sites from analysis.

Growth curves are useful tools to model patterns of growth as a function of age within and among populations and are commonly used in fisheries science but have also been applied in a wide range of mammals (e.g., Griffiths and Brook, 2005; Mumby et al., 2015; Hilderbrand et al., 2018). There are different functions for growth curves and for grizzly bears the von Bertalanffy growth function was found to be particularly parsimonious (Bartareau et al., 2011). We estimated body mass growth in grizzly bears by fitting the following function:

$$E[W|t] = W\infty \, (1 - \exp^{-k(t-t0)}), \tag{1}$$

where E[W|t] is the expected body mass at age t, W∞ is the asymptotic average maximum body mass, k is the growth coefficient, and t0 is the hypothetical age at which the average body mass is zero. We performed the curve-fitting procedure following the approach outlined by Ogle (2016), using the Levenberg-Marquardt nonlinear least-squares algorithm provided in the R package minpack.lm (Elzhov et al., 2016). Because body size in grizzly bears is dimorphic, we fitted population-level, sex-specific growth curve using data from bears born over four decades, from the 1970s through the 2010s. Measurements from same-year recaptures were excluded by randomly selecting one body composition estimation within that year, but body measurements from the same animal collected over several years were used. Regardless, the majority of the measurements were collected from grizzly bears that had only been captured once, therefore the sex-specific growth curves were assumed to be representative of the population. We identified the age at which 95% of sex-specific asymptotic lean body mass was obtained according to the von Bertalanffy growth functions, and defined growth-phase and mature bears as those younger and older than that age, respectively. We derived confidence intervals for the growth function parameters via bootstrapping (n = 999 iterations) and estimated the overall goodness-of-fit by measuring the correlation between observed and expected values. We used the Student's t-test to explore whether the individual lean body mass of bears at different life cycle stages (growth vs. mature phase) changed during 2000–2009 compared with 2010–2020 before proceeding to more complex models based on spatio-temporal, heterogeneous drivers.

Covariates

To examine the spatio-temporal relationships with local population density, we used a grizzly bear density index developed for the GYE by Bjornlie et al., (2014). The basis of that index was a spatio-temporal population reconstruction using long-term capture and telemetry data, calculated for 14- × 14-km grid cells (196 km2; approximate annual home-range of female bears) for 1983–2007, with time series projections from 2008 through 2012. Because there are no future captures from which to back-cast later years of the density index, this latter procedure was necessary to reduce underestimation due to capture lag times of approximately 5 years. Previous studies showed that the density index effectively tracked population density changes through time and space (Appendix S1 in Bjornlie et al., 2014). We used the same procedures to estimate population density from 1983 through 2015 using capture and telemetry data, and projecting trends on a cell-by-cell (n = 960) basis for 2015–2020 using ARIMA(1,1,1) forecasting based on the previous 7 years of density information

(2008–2014), accounting for drift ($d > 0$) (Hyndman and Khandakar, 2008). The spatial and temporal evolution of grizzly bear density over the GYE is shown in Figure S3. Individual variation from expected sex-specific growth, or body fat percentage, at various life stages were tested using the derived index, which allowed the assessment of local (not average) density for each individual at the time of capture.

To account for spatial heterogeneity of population dynamic processes associated with different land ownership and management, we used three geographic zones (Figure S1) as a control variable in our analysis (Supporting Information S1): Yellowstone National Park (YNP) where bears have always been present and at relatively high densities; the area outside of the national park but within the Grizzly Bear Recovery Zone (RZ) where bear densities increased during the 1990s and 2000s; and the area outside the recovery zone but within the Demographic Monitoring Area (DMA), most of which was re-occupied over the last 2 decades (Figure S1). We did not use these zones when evaluating variations in body fat percentage, because the majority of research captures in September and October were confined to Yellowstone National Park.

We controlled for the decades of 2000–2009 and 2010–2020 in our analysis as a temporal proxy for changes in the availability of high-calorie foods considered important for grizzly bears in the Greater Yellowstone Ecosystem (Supporting Information S4). Mature, cone producing whitebark pine trees (seed of which are a high caloric food source during late summer and fall for grizzly bears in the Ecosystem; van Manen et al., 2016), was experiencing extensive mortality from Mountain pine beetle (Dendroctonus ponderosae) during the first decade (2000-2009, Macfarlane et al. 2013) and had run its course by the second decade (2010-2020, Shanahan et al. 2016). Because body fat accumulation is largely a function of current conditions, whereas lean body mass is a result of past conditions, which cannot be tracked at the time of capture, we only examined the time-dependent relationship between food source availability and body fat.

Hypothesis testing

We used Generalized Additive Mixed Models (GAMMs) with a Gaussian error distribution to test our first two hypotheses (H1 and H2) by simultaneously estimating individual lean body mass (*Lean Mass*) while accounting for sex-specific growth, local grizzly bear density index, life cycle stage, and geographic zones. We used a natural log transformation for age (*Age*) and fitted it with a thin plate regression spline to match the sex-specific von Bertalanffy growth curve as accurately as possible. We then added the grizzly bear density index (*Density*) and geographic zones (*Zones*) as fixed terms, and year of capture (*Year*) as a random intercept term to account for inter-year variability (ζ). Because the density index indicated different changes over time in the three geographic zones (Figure S3), we included an interaction term (*Density x Zones*). We also included life cycle stage (*Life Stage*) as a fixed term and an interaction term between density and life cycle stage (*Density x Life Stage*) to evaluate the local density relationship of growing versus mature bears. We conditionally standardized ($\mu = 0$, $\sigma = 1$) the response variable and all continuous explanatory variables associated with each sex and checked for multicollinearity ($|r| < 0.7$, Dormann et al., 2013), thereafter fitting sex-specific GAMMs using the functions from the R package mgcv (Wood, 2011). We started by fitting the full model as:

$$\begin{gathered} Y_{\text{Lean Mass}} \sim \beta_0 + \beta_1 \log(\text{Age}) + \beta_2 \text{ Density} + \beta_3 \text{ Zones} + \beta_4 \text{ Life Stage} + \\ \beta_5 \text{ (Density x Zones)} + \beta_6 \text{ (Density x Life Stage)} + \zeta_{\text{Year}} + \varepsilon \end{gathered} \tag{2}$$

for females and males separately, then gradually reduced models, including a null model (Table S5), and assessed the relative contribution of each predictor using the second-order Akaike's information criterion (AICc). We used bootstrapping ($n = 999$ iterations) to derive confidence intervals and statistical significance for each model parameter.

We used Generalized Linear Models (GLMs) with a Gaussian error distribution to test hypotheses H3 and H4, by simultaneously estimating body composition (i.e., body fat percentage; *Body Fat*) while accounting for daily gain, local grizzly bear density index, life cycle stage, and decade of capture (i.e., 2000–2009 and 2010–2020). We began by determining the month in which the minimum body fat level is reached (i.e., the inflection point) for each sex to estimate the physiological start of the fattening period. To account for intra-year fat accumulation, we added the day of the year (*Julian*) as a fixed term and included it in all models with body fat as the response variable. We added grizzly bear density index (*Density*) and life cycle stage (*Life Stage*) as a fixed term and an interaction term (*Density x Life Stage*). Thus, we added the decade of capture (*Capture Decade*) as a fixed term and an interaction term with day of the year (*Julian x Capture Decade*) for modelling the annual rate of gain. We again included a random intercept term for year of capture (*Year*) to account for inter-year variability (ζ) and conditionally standardized ($\mu = 0$, $\sigma = 1$) the response variable and all continuous explanatory variables associated with each sex. We fitted the model as:

$$\begin{gathered} Y_{\text{Body Fat}} \sim \beta_0 + \beta_1 \text{ Julian} + \beta_2 \text{ Capture Decade} + \beta_3 \text{ Density} + \beta_4 \text{ Life Stage} + \\ \beta_5 \text{ (Julian x Capture Decade)} + \beta_6 \text{ (Density x Life Stage)} + \zeta_{\text{Year}} + \varepsilon \end{gathered} \tag{3}$$

for females and males, using individual estimates of body fat percentage from the beginning of the fat accumulation phase to the beginning of the denning season (end of October). Finally, we evaluated the relative contribution of each predictor term using the second-order Akaike's information criterion (AICc). We again used bootstrapping (n = 999 iterations) to derive confidence intervals and statistical significance for each model parameter. We performed all statistical analysis in R 4.0.0 (R Core Team, 2020) under Ubuntu 16.04.3 LTS (Canonical Ltd., London, United Kingdom).

Results

We compiled 566 (210 females, 356 males) body mass measurements for 418 individual bears (146 females, 272 males) born between 1978 and 2019 and captured for research purposes from 2000 through 2020. Monthly lean body mass of mature bears did not vary over the active season for males ($\rho = -0.06$, $p = 0.61$) and for females during June–October ($\rho = 0.11$, $p = 0.23$) (Figure S6); inclusion of May data indicated a slight trend in monthly estimates ($\rho = 0.18$, $p = 0.04$) but sample size was low (n = 8), and a higher proportion of females with dependent offspring (63%) were captured in this month, which typically have lower lean body masses than lone females (Hilderbrand et al., 2000).

The von Bertalanffy growth function accurately described the growth pattern of the Yellowstone grizzly bears, fitting both female ($\rho_{\text{female}} = 0.76$; $W\infty = 94.77 \pm 1.43$, $k = 0.39 \pm 0.05$, $t_0 = -0.44 \pm 0.30$) and male ($\rho_{\text{male}} = 0.84$; $W\infty = 161.51 \pm 3.42$, $k = 0.21 \pm 0.02$, $t_0 = -0.54 \pm 0.27$) lean body mass data well (Figure 1). Female grizzly bears grew relatively faster ($k = 0.39 \pm 0.05$) than males ($k = 0.21 \pm 0.02$), reaching 95% of their asymptotic lean body mass (90 kg) at seven years of age, whereas males reached 95% of their total lean body mass (153 kg) at the age of fourteen. When grouping bears by sex and life cycle stage, we did not observe differences in lean body mass during 2000–2009 compared with 2010–2020 (females: growing phase, $p > 0.05$; mature phase, $p > 0.05$; males: growing phase, $p > 0.05$; mature phase, $p > 0.05$) (Figure S7), ruling out simple time-dependent relationships in favor of more complex spatio-temporal drivers.

Lean body mass was positively related to age in all bears (females: $p < 0.01$; males: $p < 0.01$) (Table 2), confirming the relationship predicted by the von Bertalanffy growth function (Figure 1; see Figure S8). Despite its significance as a predictor variable in the full model, variation in lean body mass could not be explained solely by age (females: $\Delta\text{AICc} = 26.73$; males: $\Delta\text{AICc} = 16.80$, compared with best-fitting model; Table 3). Instead, female and male lean body mass were negatively related to grizzly bear population density, supporting prediction (i). Compared with models that included only lean body mass as a function of age, there was strong support for the addition of the density index covariate (females: ΔAICc = 17.49, males: ΔAICc = 16.80; Table 3) and those models were considerably more parsimonious (Table 2). Bear density had a larger effect size than any of the other predictors in the full model (females: $b_{\text{Density}} = -0.39$, $p < 0.01$; males: $b_{\text{Density}} = -0.16$, $p < 0.01$) (Table 2).

Density showed significantly stronger relationships with body mass of growing individuals than mature individuals, particularly in females (Figure 2A), partially supporting prediction (ii). When considering the full model, we observed that the effect of density on lean body mass differed between life cycle stages in females ($b_{\text{Density:Life Stage(Mature)}} = 0.32$, $p < 0.01$), but not in males ($b_{\text{Density:Life Stage(Mature)}} = 0.10$, $p > 0.05$) (Table 2). However, model selection indicated that an interaction term for females ($w = 0.93$) and, to a lesser extent, males ($w = 0.14$) should be included (Table 3), implying that male bear growth may be associated with density as well. We observed an effect size of ~20 kg difference in lean body mass among growing individuals at high versus low density, corresponding to about 20% and 12% of female and male asymptotic lean body mass, respectively.

Lean body mass did not differ across geographic areas for either sex, but was associated with the grizzly bear density index throughout the GYE. In the full model, there was no relationship between lean body mass and any of the three geographic areas (females: $b_{\text{Zones(Recovery Zone)}} = 0.08$, $p > 0.05$, $b_{\text{Zones(Yellowstone NP)}} = -0.11$, $p > 0.05$; males: $b_{\text{Zones(Recovery Zone)}} = -0.05$, $p > 0.05$, $b_{\text{Zones(Yellowstone NP)}} = -0.03$, $p > 0.05$) (Table 2) and adding geographic areas made the model less parsimonious when compared with lean body mass as a function of age (females: ΔAICc = 0.61, males: ΔAICc = 1.99) (Table 3). The relationship between lean body mass and density was generally negative in all geographic areas, with the exception of males in Yellowstone National Park (Figure 2B), which were larger at higher population densities ($b_{\text{Density:Zones(Yellowstone NP)}} = 0.22$, $p < 0.05$) (Table 2). However, bootstrapping indicated the latter relationship was only weakly supported (Figure S9.1) and should be interpreted with caution.

Exploratory analysis indicated June as the physiological start of the fattening season for all bears. Specifically, females had the lowest body fat percentage in both decades between May and June (mean = 16.%; Figure 3, top left panel), whereas males continued to lose body fat after den emergence, reaching their lowest condition in June in both decades (mean = 18.3%; Figure 3, bottom left panel). Julian date was the main variable associated with body fat percentage in females ($b_{\text{Julian}} = 0.41$, $p < 0.01$) and males ($b_{\text{Julian}} = 0.45$, $p < 0.01$) (Table 2), as evidenced by both model selection (Table 3) and bootstrapping (Figure

S9.2). According to predictions of the most parsimonious model with only Julian as fixed term, females gained 15.3 percent body fat throughout the summer to fall active season (June 1st to October 31st, 152 days; Figure 3), while males gained 16.8 percent, with daily body fat percentage increasing by 0.10 for both females and males.

Female and male body fat percentages were not related to grizzly bear population density when the full model was considered (females: $b_{\text{Densit}}y = -0.19$, $p > 0.05$; males: $b_{\text{Density}} = 0.08$, $p > 0.05$) (Table 2), nor was this relationship supported by model selection (females: ΔAICc = 2.49; males: ΔAICc = 2.62, compared with best-fitting model; Table 3), rejecting prediction (iii) and supporting the alternative hypothesis. However, bootstrapping indicated a weak negative relationship between density and body fat in females, and to a lesser extent a positive relationship in males (Figure S9.2), suggesting that the results should be interpreted with caution in this case as well. Further, population density did not have an age-dependent effect on individual body fat levels (females: $b_{\text{Density : Life Stage(Mature)}} = 0.07$, $p > 0.05$; males: $b_{\text{Density : Life Stage(Mature)}} = 0.10$, $p > 0.05$) (Table 2), as model selection also suggested (females: ΔAICc = 6.73; males: ΔAICc = 10.13, compared with best-fitting model; Table 3), rejecting prediction (iv). However, individual body fat levels did vary by life stage in females ($b_{\text{Life Stage(Mature)}} = 0.25$, $p < 0.05$), but not in males ($b_{\text{Life Stage(Mature)}} = 0.07$, $p > 0.05$) (Table 2). Although the inclusion of life stage as an explanatory variable for females was not fully supported by model selection (ΔAICc = 2.02, compared with best-fitting model; Table 3), the AICc model weight (w = 0.19) and bootstrapping (Figure S9.2) indicated that it was an important predictor when modeling body fat percentage.

Decade of capture did not show a relationship with body fat percentage. When considering the full model, we observed that Capture Decade was not affecting body fat levels (females: $b_{\text{Capture Decade(2010s)}} = -0.17$, $p > 0.05$; males: $b_{\text{Capture Decade(2010s)}} = 0.13$, $p > 0.05$) (Table 2) or gain (females: $b_{\text{Julian:Capture Decade(2010s)}} = 0.09$, $p > 0.05$; males: $b_{\text{Julian:Capture Decade(2010s)}} = 0.07$, $p > 0.05$) (Table 2) for bears captured during 2000–2009 compared with 2010–2020 (Figure 3). The inclusion of Capture Decade as a fixed term and an interaction term in the best model was further ruled out by model selection (Table 3). The bootstrapped estimates for the full model were consistent (Figure S9.2), although the proportion of variance explained by all components (fixed and random terms) was relatively lower (females: conditional $R^2 = 0.41$; males: conditional $R^2 = 0.24$) compared with models of lean body mass.

Discussion

Using individual data collected over two decades during which substantial changes in local population density occurred, together with environmental perturbations and changes in food resources, we demonstrated density-dependence effects on the body composition of the Yellowstone grizzly bears. Although body fat percentage was not clearly linked to local population density, lean body mass was found to be negatively associated with areas of higher grizzly bear density, especially for young bears, suggesting density-dependent controls on lean body mass. Previous research showed that, particularly in areas with higher bear densities, bear population growth had slowed associated with increased juvenile mortality, in which killings by adult males likely played a role, and decline in female reproductive rates (van Manen et al., 2016). Our results corroborate and integrate those findings: we suggest that intraspecific competition (i.e., interference competition) potentially limited the ability of physically immature bears, particularly females, to compete for resources with mature bears. Specifically, the increasing competition in the GYE, in the context of different local land ownership and management, had a primary effect on individual body mass. Further, a decline in several high-calorie food sources over the last two decades was observed (Gibson 2007; Gude et al., 2007; Romme et al., 2016; Supporting Information S4), yet seasonal fat accumulation rate of grizzly bears remained unaffected, supporting our alternative hypothesis that bears prioritize fat storage over lean body mass when allocating energy from food consumption. We therefore suggest that sufficient food resources were available on the landscape to accommodate successful shifts in feeding tactics in the face of perturbations and competition. Only for male bears in Yellowstone National Park we did not find evidence of a negative relationship of lean body mass with density (Figure 2B), possibly because of the abundant ungulate resources available to bears in the core area that males tend to dominate when encountered.

Our findings indicate that opportunistic large omnivores such as grizzly bears possess the behavioral and phenotypic plasticity to shift their feeding tactics in response to changes in availability of high-quality foods. However, intraspecific competition may limit the accessibility to such resources. We offer two possible explanations for this pattern: (i) grizzly bears maximize their energy intake while optimizing macronutrient consumption of proteins, carbohydrates, and lipids (Erlenbach et al., 2014; Costello et al., 2016). On a high-protein diet, bears gain mostly lean body mass, whereas consumption of low-protein foods (i.e., rich in lipids or carbohydrates) favors body fat accumulation (McLellan, 2011). Bears do, however, optimize dietary protein content while maintaining a balance of high-lipid and high-carbohydrate foods (Erlenbach et al., 2014). Despite the varied diet of grizzly bears in the Greater Yellowstone Ecosystem, much of their foraging is focused on several high-protein food resources (Gunther et al., 2014; Schwartz et al., 2014), to the extent that the population has been characterized as more carnivorous than other North American interior populations (Jacoby et al., 1999). As grizzly bear densities increased across the GYE since the 1980s, younger individuals may have experienced increasingly limited access to high-protein foods because of competition with dominant (i.e., physically mature) bears (Costello et al., 2016), resulting in reduced lean body mass. Effect sizes indicated biologically meaningful impacts especially on growing individuals (Figure 2A), with females influenced proportionally more than males (i.e., about 20% and 12% of their asymptotic lean body mass, respectively). Individual body fat percentage, on the other hand, remained constant throughout the same time period, probably because individuals were able to obtain high-lipid and high-carbohydrate foods despite increased competition; (ii) alternatively, because body fat is essential for grizzly bear hibernation and, more specifically, for female reproduction (Robbins et al., 2012) and offspring care, bears prioritize fat storage over lean body mass when allocating energy, more so than macronutrients, from food consumption. Interestingly, among females consuming a high-calorie meat diet, mass gain skewed moderately toward lean body mass in spring, but heavily toward body fat in late summer and fall (Belant et al. 2006), implying that energy allocation is prioritized for reproduction (Robbins et al., 2012). Further, in systems with super-abundant food, such as coastal Alaska, where individuals have access to high-calorie salmon, bears achieve very large body sizes (Hilderbrand et al., 1999) and accumulate substantial fat reserves. On the other hand, in areas with less abundant and more variable high-calorie foods, bears are generally characterized by smaller body sizes, but often accumulate body fat in proportions similar to their large relatives (Hilderbrand et al., 2018). This could suggest that, except for systems overwhelmed with high-calorie food (i.e., coastal Alaska), bears first allocate excess energy to building up and maintaining an adequate store of fat, and then use the rest to increase lean body mass to achieve larger body size. Collectively, evidence suggests the dietary plasticity of grizzly bears allows individuals to achieve similar body condition (i.e, percent body fat) despite dietary variation that results in substantial disparities in total lean body mass (Belant et al. 2006, Mangipane et al. 2017, Hilderbrand et al. 2018). Still, dietary plasticity may be insufficient to compensate for severe landscape-level reductions in food availability, at which point grizzly bears would likely be unable to maintain typical body condition, especially in areas where interference competition reduces foraging efficiency.

In the core area of the GYE (i.e., the Yellowstone National Park), lean body mass of males did not depend on density, which may find an explanation in the relation between food types and dominance. One of the most abundant source of proteins for grizzly bears is wild ungulates, particularly bison, which occur in higher numbers in the Yellowstone National Park (Gunther et al., 2014). This widespread accessibility to a high-protein food resource (both as prey and carrion) may decrease the local competition for food in males. Alternatively, the dominant animals may induce dispersal of competitors and smaller, presumably younger, individuals outside of Yellowstone core area. This is consistent with the observation that population density in the core area has stabilized in the recent decade and population is currently expanding outwards in the GYE (Figure S3; Bjornlie et al., 2014).

The age at which females and males reached 95% of the asymptotic lean body mass coincided with their reproductive strategies. Between the ages of four and seven, all nulliparous females observed in this study had produced cubs. Conversely, males, although sexually mature by age four, do not reach their reproductive prime until they reach sufficient body mass to support rivalry and endurance competition for breeding opportunities (Schwartz et al., 2006; Zedrosser et al., 2007). Our results showed that the capital breeding strategy (Jönsson, 1997; Stephens, et al., 2009) of Yellowstone grizzly bears was maintained throughout the study period and associated environmental changes (Gibson 2007; Gude et al., 2007; Romme et al., 2016; Supporting Information S4). Reproductive-age females are gaining adequate body fat in the GYE to support pregnancy and lactation while denned (Robbins et al., 2012). Adult male bears instead seem to finance reproduction by allocating capital, namely fat, prior to hibernation (i.e., previous-year hyperphagia), as they continue to lose body fat for several months after den emergence, associated with the subsequent breeding season (Figure 3, bottom left panel). This likely occurs because food sources are scarce and dispersed in the spring, large-bodied bears have a limited intake rate and physiological capacity when subsisting on low-energy plant foods (McLellan, 2011; Costello et al., 2016), and males travel extensively searching for mates. Males thus use stored energy reserves during spring, and start allocating energy once higher-calorie foods become available in summer and fall. In animal populations nearing carrying capacity and with shifting resources, phenotypic correlations may provide a useful assessment of animals' performance (Festa-Bianchet et al., 1998). Patterns of fat accumulation over the active season did not change from 2000–2009 to 2010–2020 and were consistent with previous findings (Schwartz et al., 2014). Whereas high population density and resulting interference competition may contribute to low-protein diets among individuals in their growing phase, our analyses suggest neither intraspecific mechanisms or environmental changes are currently limiting consumption of foods high in lipids or carbohydrates for fat accumulation, and thus individual performance.

Our results do not indicate that changes in body composition of grizzly bears occurred over a two-decade period during, and following changes in the relative spatio-temporal availability of high-quality food sources (Gibson 2007; Gude et al., 2007; Romme et al., 2016; Supporting Information S4). However, more extreme perturbations may occur in the future that could strengthen density-independent effects. For example, the GYE is experiencing a profound warming trend that started in the 2000s (Heeter et al., 2021), and continued warming could increase thermal constraints on energy expenditure of reproductive females in the future (Rogers et al., 2021). In parallel, exurban development has increased in the GYE (Gude et al., 2007), and is particularly expected to continue in regions with more protected lands (McDonald et al., 2007). These density-independent effects could, in a feedback mechanism, gradually limit resource availability, lowering carrying capacity and reinforce density-dependent effects. So far, grizzly bears seem to have sufficient space to disperse and hence shift food sources when competition arises. However, the resulting range expansion has also led to increased conflict potential (e.g., livestock depredation) on the periphery of occupied range, where anthropogenic influences on the landscape are greater. Hence, the ability of the GYE to support an expanding grizzly bear population with high indices of performance will depend on a combination of the following factors: (i) the plasticity in the use of trophic resources; (ii) the availability of natural, high-quality foods; and (iii) the possibility for the population to spatially expand, thus decreasing interference competition. Although we recorded a marked plasticity among GYE grizzly bears to maintain body condition across environmental gradients and during, and following a period with declines in several high-quality foods, density-dependent effects may increasingly affect accessibility to resources, for example due to limits to population expansion or resource-poor landscapes. Furthermore, as the grizzly population grows, individual dispersal (which is critical for the population's long-term survival) may increase conflicts and consequently individual mortality, particularly in more human-dominated environments. Local monitoring seems to support this, since demography appears to be primarily driven by intraspecific factors within the core area, whereas anthropogenic factors (i.e., mortality) seem to primarily affect demography on the periphery of the population (van Manen, et al., 2020). The ability to recognize demographic changes and whether they are driven by density-dependent or density-independent effects, allows for informed and timely decision-making for species of conservation concern (Mccarthy and Possingham, 2007).

By studying one of the world's largest terrestrial omnivores, we showed that generalist species (i.e., euryphagous) have the ability to modify feeding tactics in response to density-dependent factors while accounting for density-independent perturbations. Generalists have an evolutionary advantage in environments with fluctuating nutrients because they can maintain loose links with numerous food sources (Pimm, 1982; Kratina et al., 2012) by optimizing their foraging while exhibiting multi-food source functional responses (Morozov and Petrovskii, 2013). Because of their ability to buffer short-term changes in habitat production, density-independent perturbations are unlikely to have a strong direct effect as in specialists. Individual performance of large-bodied omnivores (as well as medium-bodied omnivores; Kruuk and Parish, 1982; Dennis and Otten, 2000) is, however, influenced by increased population density and competition for limited resources. Omnivores without territorial boundaries could track and acquire high-quality food sources based on local availability (either in terms of calories or macronutrients), resulting in individuals competing in areas with higher availability of food but, as a result, higher local population density. Life-stage, sex, and species-specific social mechanisms, such as female philopatry and dominance, could play a role too in resource acquisition in high density area for large omnivores. In contrast to specialist species, however, these mechanisms will predominantly drive individual performance when local density is high, and will be less relevant when food resources fluctuate. Only in extreme landscape-level reductions in food availability may plasticity be insufficient to compensate for these changes, at which point individuals are likely to be unable to maintain typical body condition, particularly in areas where interference competition reduces foraging efficiency.

The behavioral adaptations in tactics of omnivores to landscape-wise resource availability, together with changes in life-history traits as a result of interference competition, are considered to be the conditions necessary for omnivory to be stabilizing (Kratina et al., 2012). Furthermore, guilds of large omnivores generally exhibit a variety of other niche and phenotype features, such as ecosystem engineering or niche construction behaviors, that provide critical ecosystem functions (Root-Bernstein and Ladle, 2019). Through eco-evolutionary feedback, the functional role of large omnivores in their environment is dynamically linked to the evolution of their function (Post and Palkovacs, 2009). For instance, the relative abundance of plants and prey can influence an animal's feeding strategy (i.e., from herbivory to carnivory), whereas higher habitat productivity generally promotes omnivory, particularly of higher trophic levels (Chubaty et al., 2014). On the other hand, because omnivory is a pattern of phenotypic expression determined by environmental conditions rather than a fixed strategy (Chubaty et al., 2014), competition for scarce resources results in evolutionary-regulated intraspecific adaptations, which drive eco-evolutionary feedbacks even further.

There is growing concern about ecosystems reaching tipping points as a result of landscape-level disruptions, with potentially destabilizing effects on populations or entire communities (Dakos et al., 2019). In the short term, the presence of large and long-lived omnivores may help offset the consequences of such landscape-level perturbations. However, if perturbations persist and more extreme and abrupt events such as wildfires, severe heatwaves, or rapid land use changes significantly reduce habitat productivity, environmental pressure may promote evolutionary shifts in feeding strategy within the community (from generalist to specialist; Chubaty et al., 2014), resulting in a temporary loss of resilience. Omnivores require a diverse and productive ecosystem to flourish, just as the ecosystem requires the existence of omnivores to fully function. In a rapidly changing world, it will be critical to understand these eco-evolutionary feedbacks in order to assess the state of the ecosystem, not only for omnivores, but for all species.

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Tables and figures

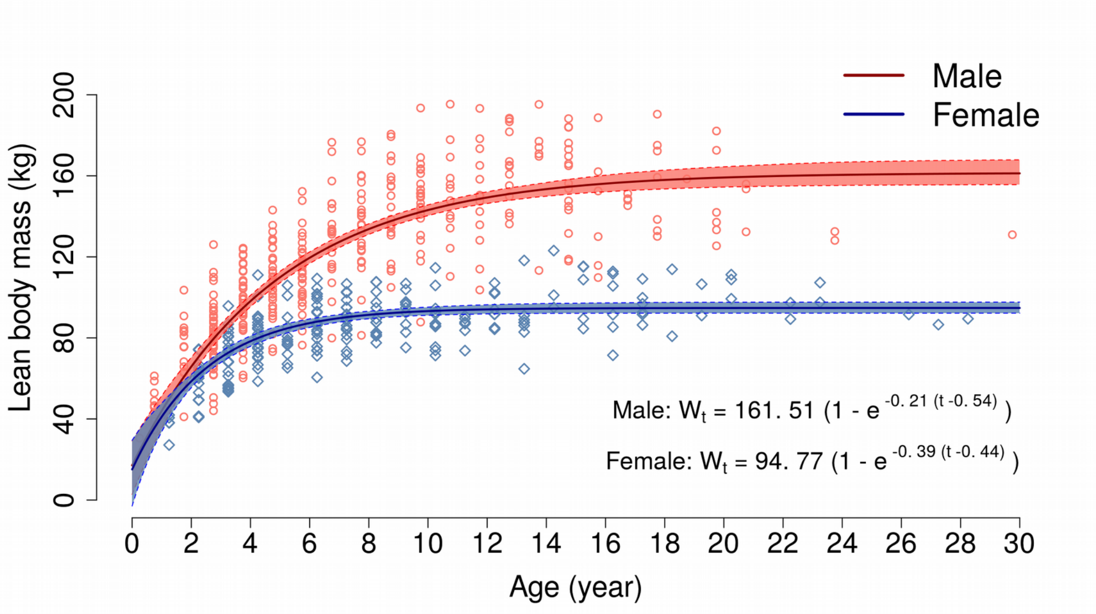


Figure 1 - Sex-specific von Bertalanffy growth curves fitted to lean body mass (kg) and age (year) data of grizzly bears from research captures in the Greater Yellowstone Ecosystem during 2000–2020. Each symbol (blue diamond for females, red circle for males) represents an individual lean body mass measurement (146 females, 272 males) collected between 2000 and 2020. The solid lines (blue for females, red for males) indicate the von Bertalanffy growth function fitted to the data, whereas corresponding shaded areas represent the 95% confidence intervals estimated via bootstrapping (n = 999 iterations). The sex-specific von Bertalanffy growth equations are shown for reference (right bottom).

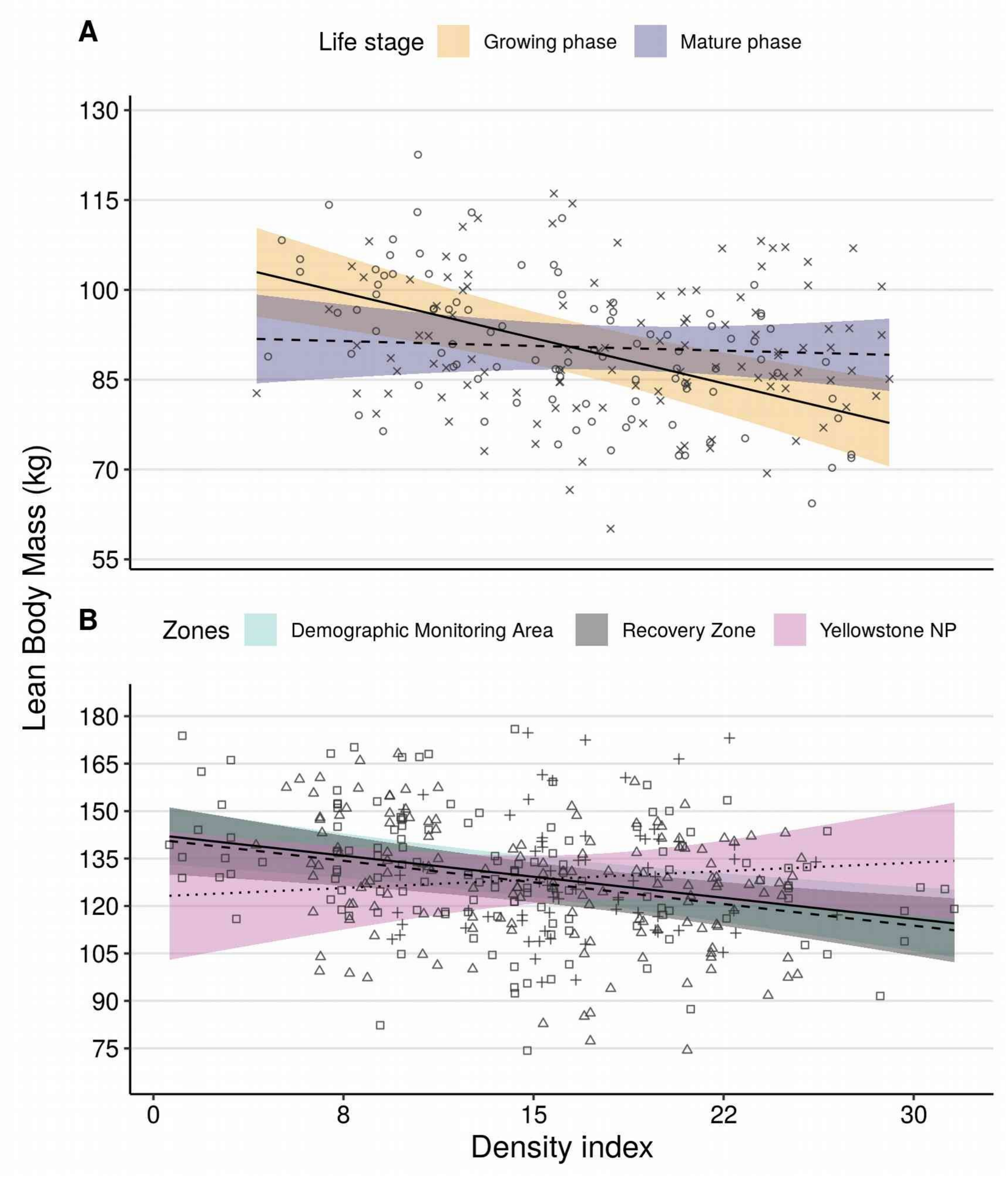


Figure 2 - **A:** Fitted regression lines with 95% confidence bands, estimated via Generalized Additive Mixed Models, of the empirical relationship between lean body mass, grizzly bear density index, and life cycle stage (growing vs. mature individuals, shown in yellow and purple, respectively) based on research captures of female grizzly bears in the Greater Yellowstone Ecosystem during 2000–2020. We defined mature female bears from the age of 7. Each symbol (circle for growing individuals, cross for mature individuals) represents an individual measurement of lean body mass. The regression coefficients are derived from the full model (Table 2). **B:** Fitted regression lines with 95% confidence bands, estimated via

Generalized Additive Mixed Model, of the empirical relationship between lean body mass, grizzly bear density index, and geographic areas based on research captures of male grizzly bears in the Greater Yellowstone Ecosystem during 2000–2020. Each symbol (square for Demographic Monitoring Area, triangle for Recovery Zone, and plus for Yellowstone National Park) represents an individual measurement of lean body mass. The regression coefficients are derived from the full model (Table 2). The visualization is based on the visreg package in R (Breheny and Burchett, 2017).

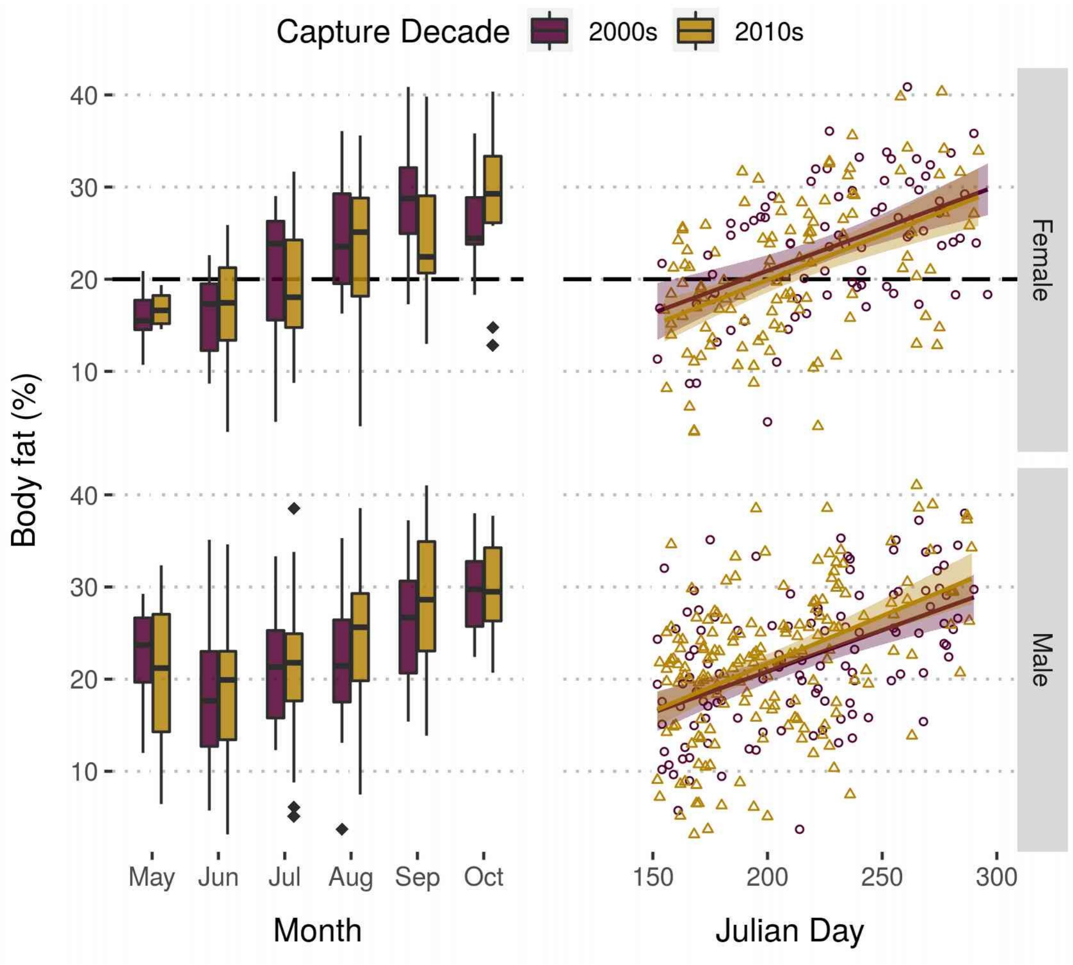
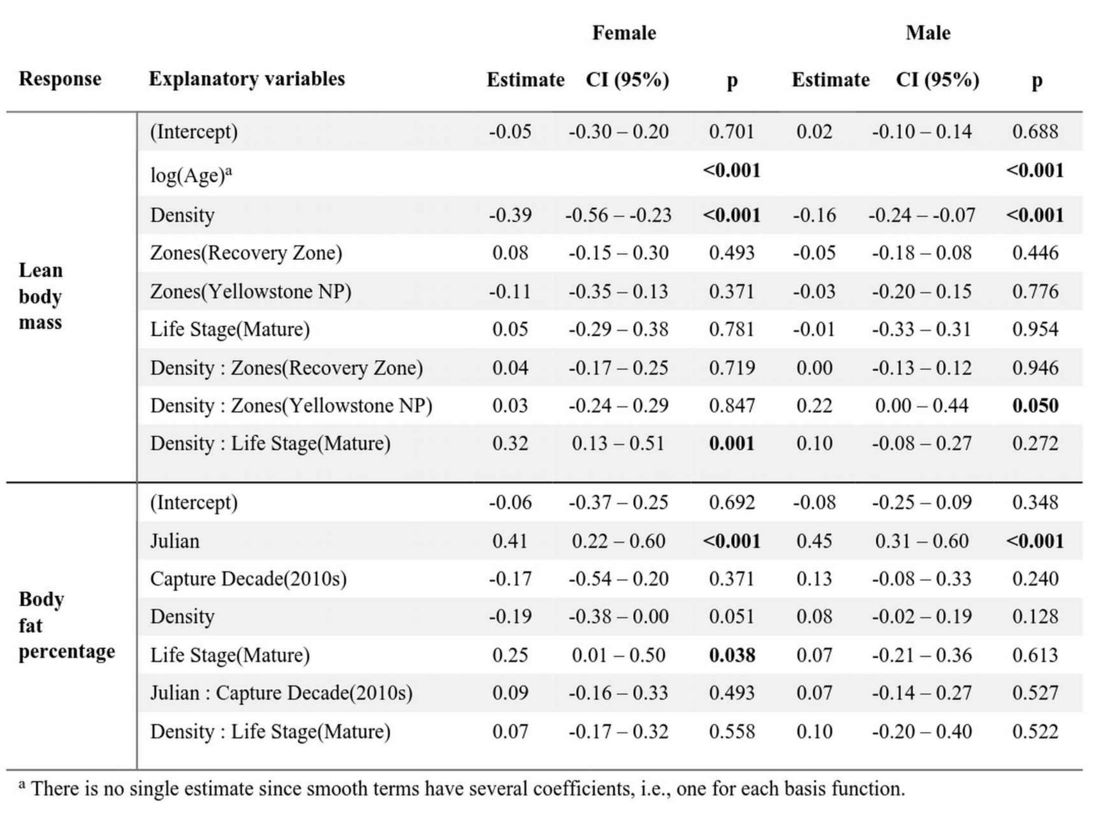


Figure 4 - LEFT: Boxplots of percent body fat from May to October of independent-age (≥2 yrs) grizzly bears captured in the Greater Yellowstone Ecosystem over two decades (2000–2009 and 2010–2020). RIGHT: Fitted regression lines and 95% confidence bands for the empirical relationship between percent body fat and Julian day over two decades, from June (physiological start of the fattening season) to October (beginning of the denning season). Each symbol (purple circle for 2000–2009, dark yellow triangle for 2010–2020) represents an individual measurement of body fat percentage. On top plots, the horizontal dashed line marks the 20% threshold required for females to support reproduction (Robbins et al., 2012). We divided predictions into capture decades (which were not included in the best model, as indicated by the model selection) to show how body mass and composition remained consistent across time.

Table 1- Hypotheses and predictions tested in the study on population-scale drivers of individual grizzly bear body mass and composition, together with the ecological principles that led to their formulation.

ECOLOGICAL PRINCIPLE		***HYPOTHESIS***	***PREDICTION***	***SUPPORTED***
DENSITY-DEPENDENT EFFECTS INFLUENCE INDIVIDUAL BODY MASS IN LARGE MAMMALS	H1	Individual grizzly bear lean body mass declines as population density increases	(i) Lean body mass of bears is negatively related to grizzly bear population density	Yes
DENSITY-DEPENDENT EFFECTS ARE STRONGER FOR GROWING THAN MATURE INDIVIDUALS IN MAMMALS	H2	Population density has an age-dependent effect on lean body mass	(ii) Lean body mass of growing individuals, more so than mature individuals, is negatively related to population density	Only for females
BODY COMPOSITION OF OMNIVORES IS AFFECTED BY DENSITY-DEPENDENT EFFECTS	H3	Individual grizzly bear body fat level decrease as population density increases and remains constant across decades characterized by different resource availability	(iii) Body fat percentage is negatively related to grizzly bear population density, irrespectively of food resource variation across decades	No
DENSITY AFFECT BODY COMPOSITION OF GROWING INDIVIDUALS MORE THAN MATURE INDIVIDUALS	H4	Population density has an age-dependent effect on individual body fat levels	(iv) Body fat percentage of growing individuals, more so than mature individuals, is negatively related to population density	No

Table 2 - Results of fitted full GAMMs of lean body mass and GLMMs of body fat percentage of female and male grizzly bears in the Greater Yellowstone Ecosystem, 2000–2020. For each sex-specific model, the response and explanatory variables, parameter estimates (conditionally standardized), 95% confidence intervals for the estimates, and p-values are reported. The Demographic Monitoring Area, Growing Phase, and 2000s (2000-2009) are the reference categories for the categorical variables Zones, Life Stage, and Capture Decade, respectively.



		Female			**Male**		
Response	**Explanatory variables**	**Estimate**	**CI (95%)**	**p**	**Estimate**	**CI (95%)**	**p**
Lean body mass	(Intercept)	-0.05	-0.30 – 0.20	0.701	0.02	-0.10 – 0.14	0.688
	log(Age)[a]			**<0.001**			**<0.001**
	Density	-0.39	-0.56 – -0.23	**<0.001**	-0.16	-0.24 – -0.07	**<0.001**
	Zones(Recovery Zone)	0.08	-0.15 – 0.30	0.493	-0.05	-0.18 – 0.08	0.446
	Zones(Yellowstone NP)	-0.11	-0.35 – 0.13	0.371	-0.03	-0.20 – 0.15	0.776
	Life Stage(Mature)	0.05	-0.29 – 0.38	0.781	-0.01	-0.33 – 0.31	0.954
	Density : Zones(Recovery Zone)	0.04	-0.17 – 0.25	0.719	0.00	-0.13 – 0.12	0.946
	Density : Zones(Yellowstone NP)	0.03	-0.24 – 0.29	0.847	0.22	0.00 – 0.44	**0.050**
	Density : Life Stage(Mature)	0.32	0.13 – 0.51	**0.001**	0.10	-0.08 – 0.27	0.272
Body fat percentage	(Intercept)	-0.06	-0.37 – 0.25	0.692	-0.08	-0.25 – 0.09	0.348
	Julian	0.41	0.22 – 0.60	**<0.001**	0.45	0.31 – 0.60	**<0.001**
	Capture Decade(2010s)	-0.17	-0.54 – 0.20	0.371	0.13	-0.08 – 0.33	0.240
	Density	-0.19	-0.38 – 0.00	0.051	0.08	-0.02 – 0.19	0.128
	Life Stage(Mature)	0.25	0.01 – 0.50	**0.038**	0.07	-0.21 – 0.36	0.613
	Julian : Capture Decade(2010s)	0.09	-0.16 – 0.33	0.493	0.07	-0.14 – 0.27	0.527
	Density : Life Stage(Mature)	0.07	-0.17 – 0.32	0.558	0.10	-0.20 – 0.40	0.522

[a] There is no single estimate since smooth terms have several coefficients, i.e., one for each basis function.

Table 3 - Model selection results for models of lean body mass and body fat percentage of female and male grizzly bears in the Greater Yellowstone Ecosystem, 2000–2020. The response and explanatory variables, deviance, second-order Akaike's Information Criterion (AICc) scores, delta AICc (ΔAICc), and AICc model weight (*w*) are reported for each model. Models are ranked by AICc scores and weight for each response variable and sex.

Response	**Sex**	**Explanatory variables**[a]	**Deviance**	**AICc**	**ΔAICc**	***w***
Lean Body Mass	**Female**	log(Age) + Density + Life Stage + Density : Life Stage	74.96	393.71	0	0.93
		log(Age) + Density + Zones + Life Stage + Density : Zones + Density : Life Stage	73.78	399.16	5.45	0.06
		log(Age) + Density	78.14	402.95	9.24	0.01
		log(Age) + Density + Zones + Density : Zones	77.83	406.08	12.37	0
		log(Age)	84.31	420.44	26.73	0
		log(Age) + Zones	83.92	420.81	27.10	0
		log(Age) + Life Stage	84.34	422.11	28.40	0
		~ 1	195.59	591.49	197.78	0
	Male	log(Age) + Density	92.68	556.69	0	0.63
		log(Age) + Density + Zones + Density : Zones	90.22	559.01	2.32	0.20
		log(Age) + Density + Life Stage + Density : Life Stage	92.59	559.77	3.08	0.14
		log(Age) + Density + Zones + Life Stage + Density : Zones + Density : Life Stage	90.10	562.28	5.59	0.04
		log(Age)	97.58	573.49	16.80	0
		log(Age) + Life Stage	97.70	575.63	18.94	0
		log(Age) + Zones	97.03	575.77	19.08	0
		~1	326.39	993.55	436.86	0
Body Fat Percentage	**Female**	Julian	473.42	488.21	0	0.51
		Julian + Life Stage	470.93	490.23	2.02	0.19
		Julian + Density	470.03	490.70	2.49	0.15
		Julian + Capture Decade	472.83	491.16	2.95	0.12
		Julian + Capture Decade + Julian : Capture Decade	472.11	494.80	6.59	0.02
		Julian + Density + Life Stage + Density : Life Stage	465.26	494.94	6.73	0.02
		Julian + Capture Decade + Density + Life Stage + Julian : Capture Decade + Density : Life Stage	464.05	501.82	13.61	0
		~1	530.89	539.63	51.42	0
	Male	Julian	751.90	768.23	0	0.61
		Julian + Density	748.32	770.85	2.62	0.17
		Julian + Capture Decade	750.51	771.57	3.34	0.12
		Julian + Life Stage	751.65	772.06	3.83	0.09
		Julian + Capture Decade + Julian : Capture Decade	750.14	775.96	7.73	0.01
		Julian + Density + Life Stage + Density : Life Stage	747.73	778.36	10.13	0
		Julian + Capture Decade + Density + Life Stage + Julian : Capture Decade + Density : Life Stage	745.85	786.09	17.86	0
		~1	827.66	837.58	69.35	0

[a] Year of capture was always included as a random intercept term in the model formula

Supplementary Material

S1. Landscape zoning within the Greater Yellowstone Ecosystem

Yellowstone National Park is 8,991 km^2 and represents the core of the grizzly bear distribution in the ecosystem. Visitor access is regulated and over 90% of the national park is managed as wilderness. The U.S. Fish and Wildlife Grizzly Bear Recovery Zone is an area with 98.5% federal land ownership that is centered on Yellowstone National Park and within which specific grizzly bear habitat protections are in place (U.S. Fish and Wildlife Service, 1993). The portion of the Recovery Zone outside Yellowstone National Park is managed for multiple use, primarily by the U.S. Forest Service. Finally, the boundary encompassing the largest extent is the Demographic Monitoring Area (49,931 km^2), which represents the area defined as suitable grizzly bear habitat plus narrow areas along valley bottoms bounded by suitable habitat that could act as potential mortality sinks (Interagency Grizzly Bear Study Team, 2013). The Demographic Monitoring Area defines the extent of the area of population monitoring for which demographic criteria are evaluated annually (U.S. Fish and Wildlife Service, 2013).

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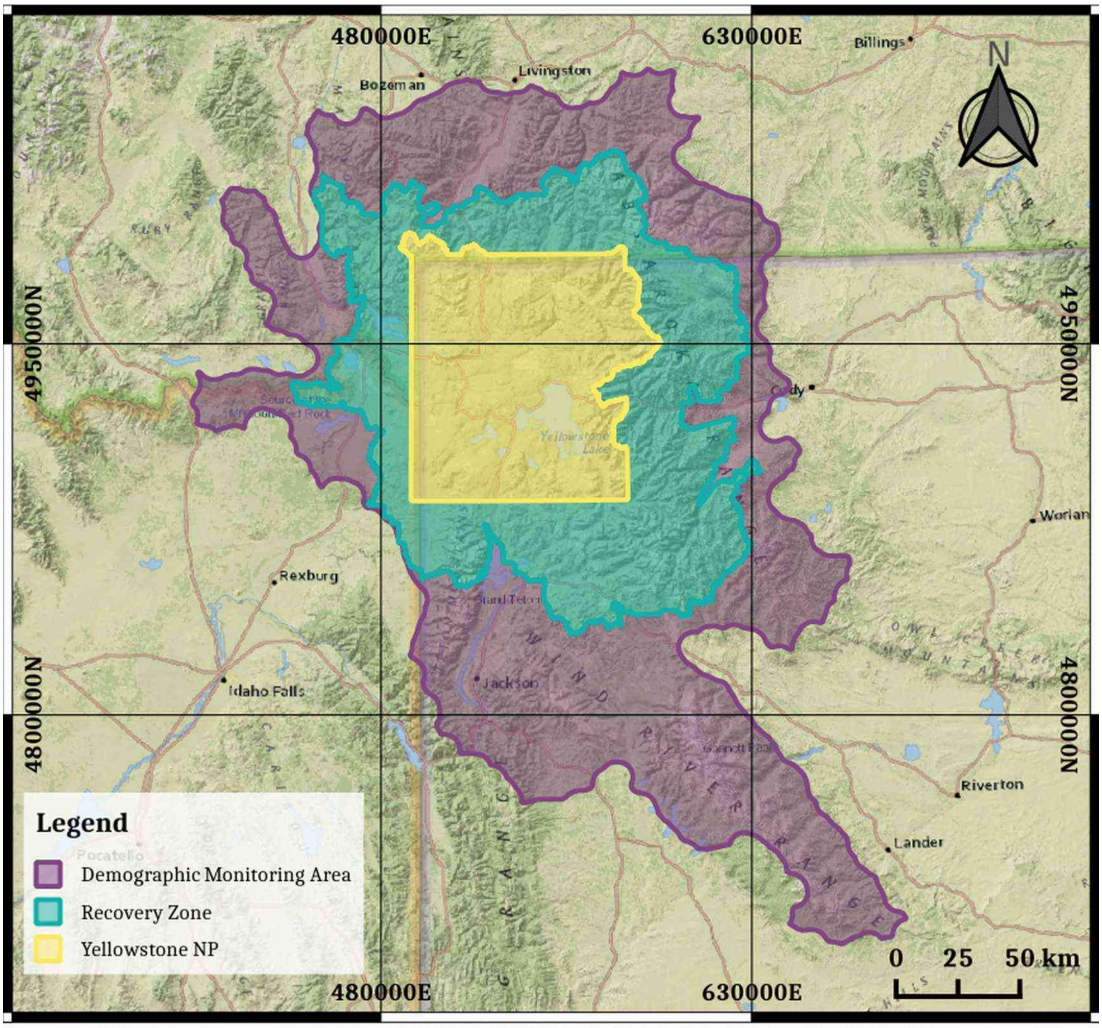

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Figure S1 - The primary areas for management regimes and landscape characteristics in the Greater Yellowstone Ecosystem. The Demographic Monitoring Area, delineated in purple, is the area where the bear population is monitored and demographic criteria are assessed on an annual basis. The Grizzly Bear Recovery Zone (as designated by the U.S. Fish and Wildlife Service), delineated in turquoise, is the area within the Demographic Monitoring Area where strict grizzly bear habitat protections are in effect. The Yellowstone National Park, delineated in yellow, is a federally protected area that includes the core of grizzly bear distribution within the Recovery Zone.

S2. Grizzly bear lean body mass in relationship to carcass redistribution sites proximity

Road-killed ungulates are collected and transported to carcass redistribution sites in Yellowstone and Grand Teton National Parks and grizzly bears have access to these temporary, highly concentrated trophic sources. Adult male grizzlies have been observed to dominate these highly caloric and predictable food sources. In order to rule out any potential confounding effects, we investigated whether lean body mass (in kilograms) was correlated with the proximity (in meters) of carcass redistribution sites. Firstly, we collected information on 13 carcass redistribution sites, including the spatial distribution and usage, between Yellowstone and Grand Teton National Parks. Then, we obtained the residual value from the mode fit of each data point using sex-specific von Bertalanffy growth curves (as described in the manuscript). Next, using a 250m moving threshold, we divided the dataset iteratively between grizzly bears captured within and grizzly bears captured outside a threshold distance of an active carcass redistribution site (from 250m to 5,000m). Last, we performed Student's t-tests for each threshold to see if there was a statistically-significant difference in lean body mass between the two groups' means. To minimize autocorrelation, we randomly selected one data point per individual grizzly bear (some bears have been captured multiple times in their lifetime). We repeated the procedure 1000 times and calculated mean and 95% confidence interval for statistical significance. Our results suggest that male grizzly bears trapped within 1,500 meters from an active carcass redistribution site were significantly larger than those trapped further away, as shown in Figure S2, whereas we did not find any significant difference in weight for females. For our morphometric study, we discarded all males captured within 2,000 meters of an active carcass redistribution site due to a clear departure from significance at that threshold (Figure S2).

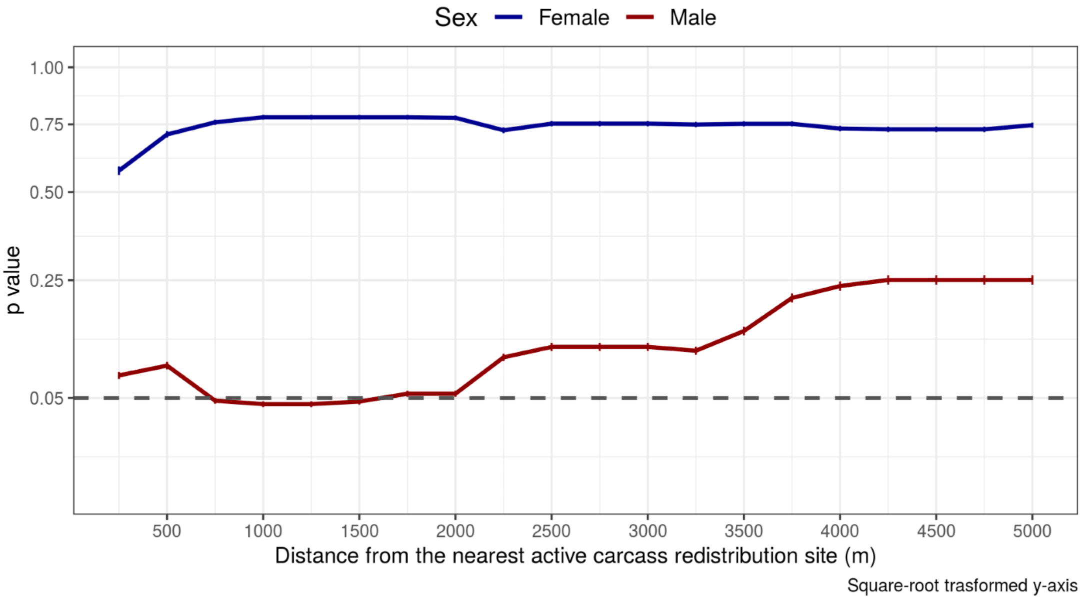

Figure S2 - Statistical threshold for confounding relationship between lean body mass (in kg) and carcass redistribution site proximity (in meters). For each distance, the t-test p-value for the difference in lean body mass between the two groups' means (grizzly captured within and outside a given distance of an active carcass redistribution site) is reported.

S3. Temporal change in bear density in the Greater Yellowstone Ecosystem

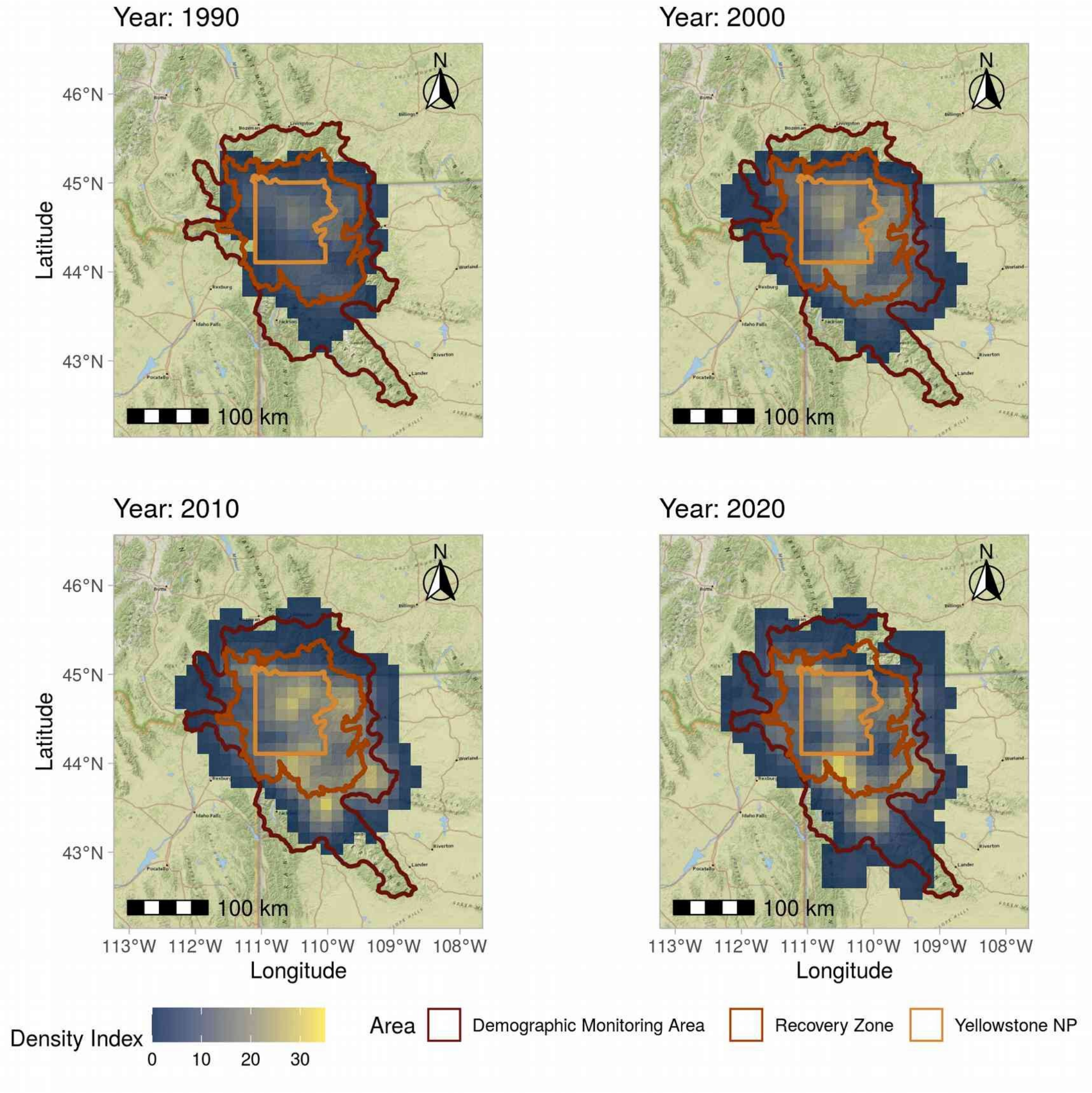

Figure S3 - Changes in bear density index in the three different geographic zones from 1990 to 2020. The grizzly bear population density was calculated on a pixel-by-pixel basis (196 km^2 square grid) for the entire Greater Yellowstone Ecosystem using the method described by Bjornlie et al. (2014).

S4. Temporal changes in high-calorie food availability

Changes in high-calorie food availability throughout time

The available food resources for the Yellowstone grizzly bear population have changed in recent years. We used the decade of capture (2000–2009 and 2010–2020) as a temporal proxy of resource distribution in the Greater Yellowstone Ecosystem to track such temporal changes. Ungulate resources (primarily elk and bison) increased after cessation of ungulate reduction programs of the 1960s. However, elk populations declined with the gray wolf reintroductions in 1995. Cutthroat trout, a valuable food for grizzly bears residing near the tributary streams to Yellowstone Lake (Reinhart and Mattson, 1990), increased after limits were imposed on take in the 1960 and through the late 1990s. However, predation by non-native lake trout (*Salvelinus namaycush*), whirling disease (*Myxoblus cerebralis*), and prolonged droughts (Koel et al. 2003; 2005) have caused major declines in subsequent decades. The cutthroat trout population is estimated to be <10% of historical numbers (Koel et al., 2005) and biomass of cutthroat trout consumed by grizzly bears and American black bears (*Ursus americanus*) in this region declined by 70% and 95%, respectively, between 1997 and 2007 (Fortin et al., 2013). Finally, whitebark pine was impacted by expansive fires in 1988 and subsequent fires. Starting in the early 2000s, whitebark pine also experienced widespread tree mortality because of mountain pine beetle (*Dendroctonus ponderosae*) and white pine blister rust (*Cronartium ribicola*), with mountain pine beetle having caused the greatest mortality (Gibson 2007; Shanahan et al., 2016). In the Greater Yellowstone Ecosystem, food availability was higher in the first decade of capture (2000-2009) than in the second decade (2010-2020), particularly with whitebark pine declining significantly in the latter ten years.

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S5. Estimated parameters and significance levels computed with bootstrapping

Table S5 - The set of parameters in each model (from full to null, including reduced models) that was used to determine the relative contribution of each predictor via model selection for prediction (i-ii; Lean body mass) and (iii-iv; Body fat percentage).

	Explanatory variable	Full	Reduced 1	Reduced 2	Reduced 3	Reduced 4	Reduced 5	Reduced 6	Null
Lean mass	(Intercept)	x	x	x	x	x	x	x	x
	log(Age)	x	x	x	x	x	x	x	
	Density	x	x	x			x		
	Zones	x	x			x			
	Life Stage	x		x	x				
	Density : Zones	x	x						
	Density : Life stage	x		x					
	1|Year	x	x	x	x	x	x	x	x
Body fat	(Intercept)	x	x	x	x	x	x	x	x
	Julian	x	x	x	x	x	x	x	
	Capture Decade	x	x				x		
	Density	x		x		x			
	Life stage	x		x	x				
	Julian : Capture Decade	x	x						
	Density : Life stage	x		x					
	1|Year	x	x	x	x	x	x	x	x

S6. Lean body mass of mature bears throughout the active season

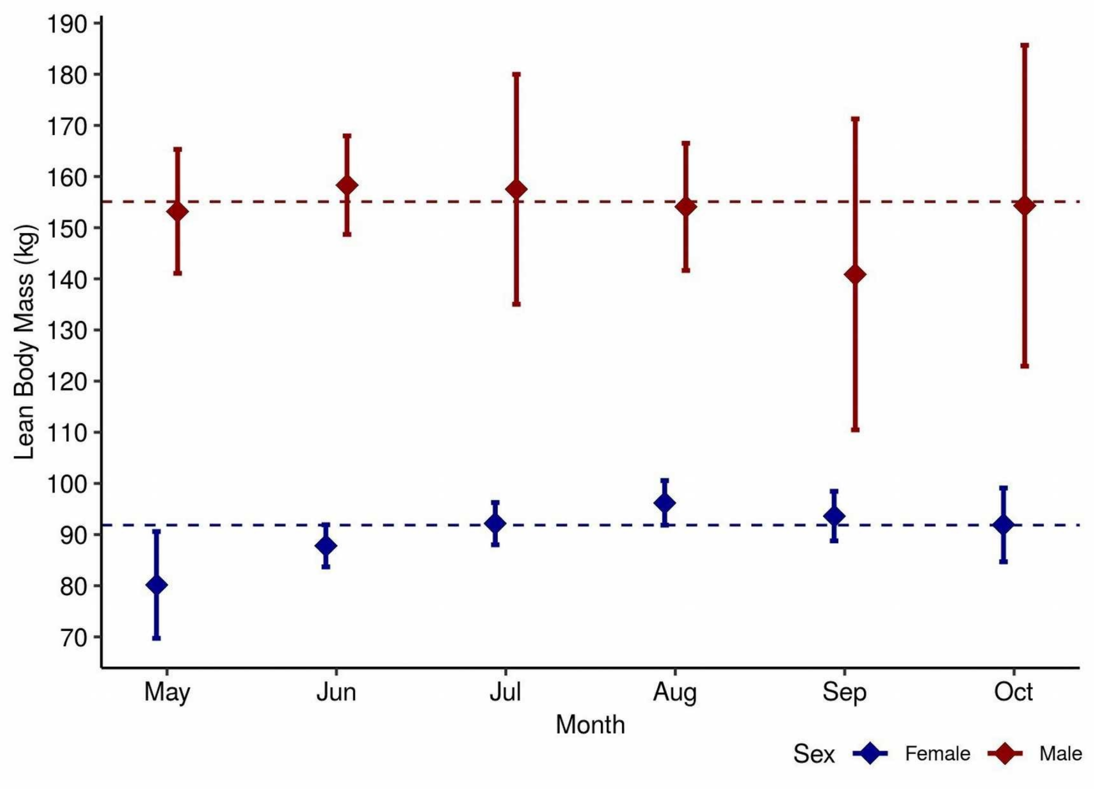

Figure S6 - Mean lean body mass (in kg) and 95% confidence intervals of bears that have reached 95% of their maximum weight (female: ≥7 years old, male: ≥14 years old), from May to October. The dashed lines (blue for females, red for male) represent the overall mean.

S7. Overall difference in lean body mass between life cycle stage

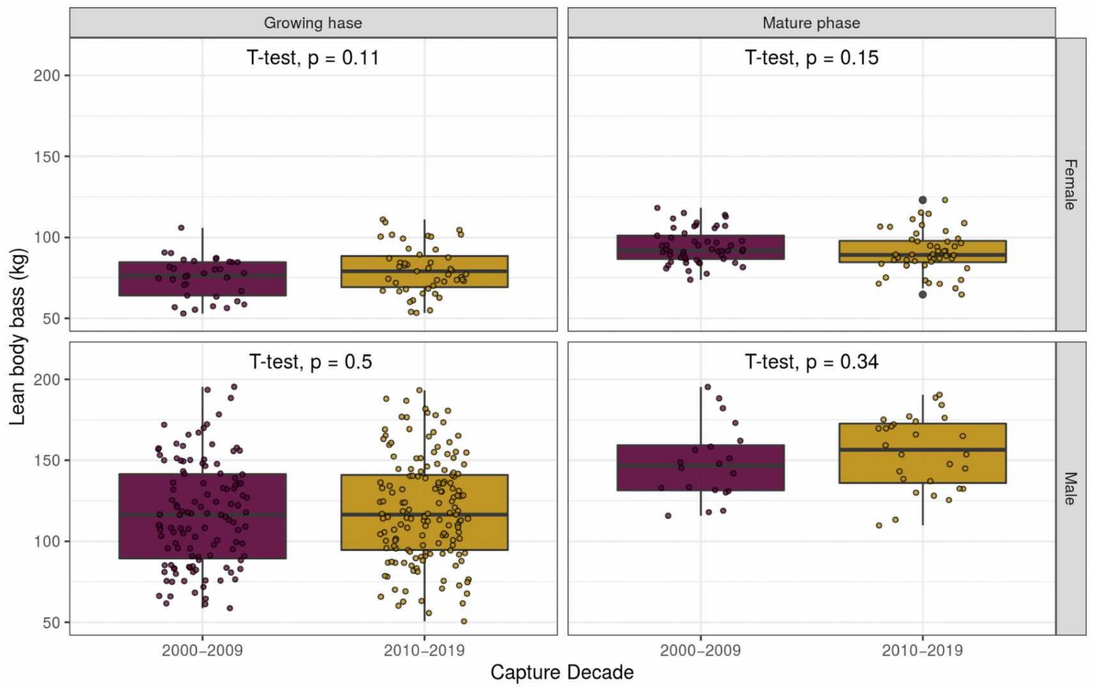

Figure S7 - Boxplots of lean body mass (in kg) in female and male grizzly bears at each life cycle stage (growth and mature phase) and throughout two capture decades (2000–2009 and 2010–2019). In each panel, the t-test p-values are displayed to highlight the statistical difference between groups.

S8. Visualization of the regression models

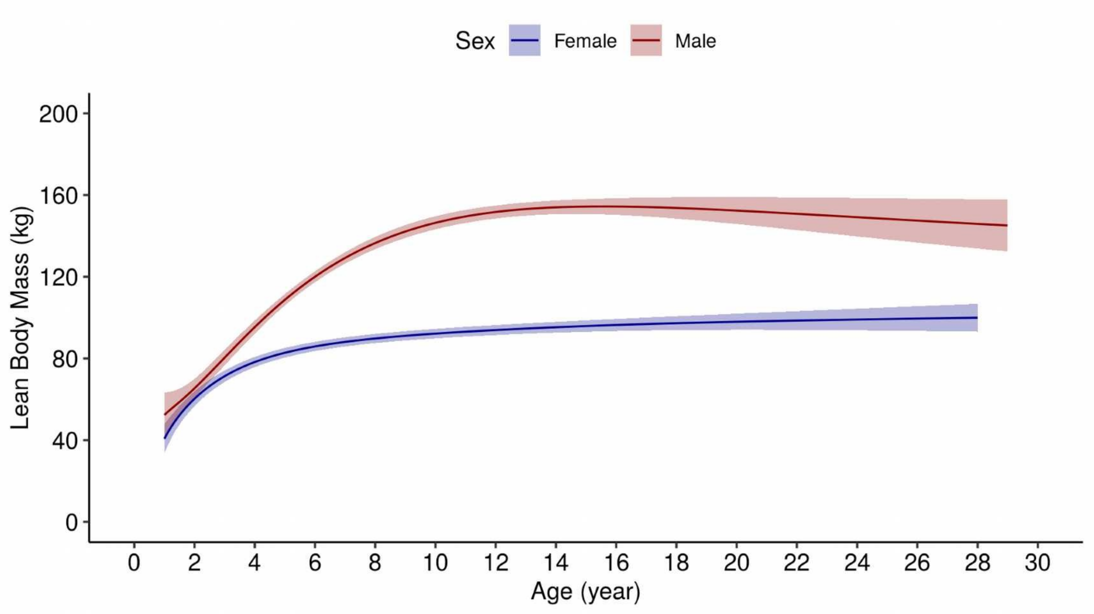

Figure S8 - Fitted regression line (with 95% confidence bands) of the empirical relationship between lean body mass and grizzly bear density index estimated via generalized additive mixed model. The regression coefficients are derived from the full model. The visualization is based on the visreg package in R (Breheny and Burchett, 2017).

S9. Estimated parameters and significance levels computed with bootstrapping

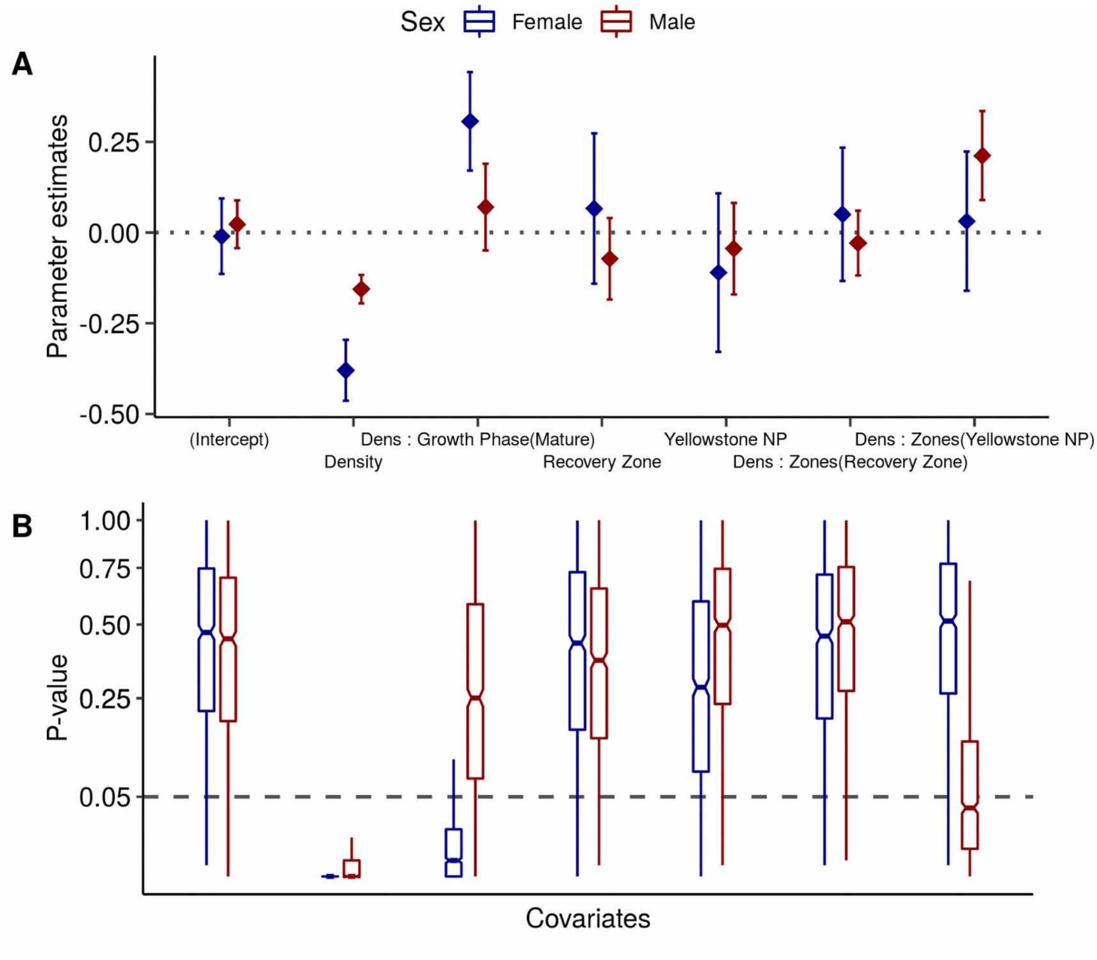

Figure S9.1 - A: Bootstrapped regression coefficients (mean ± 1 SD) of the fitted full model performed for post hoc analysis. Geographic areas were included in the full model for predictions (i) and (ii) to control for local land ownership and management. The dotted line marks the zero. B: P-value distributions of bootstrapped model's parameters for predictions (i) to (iii). The dashed line marks the statistical significance level (p = 0.05) and the boxplot notch the 95% confidence interval of the median. The y-axis is scaled (by square root transformation) to highlight the values near the reference significance level.

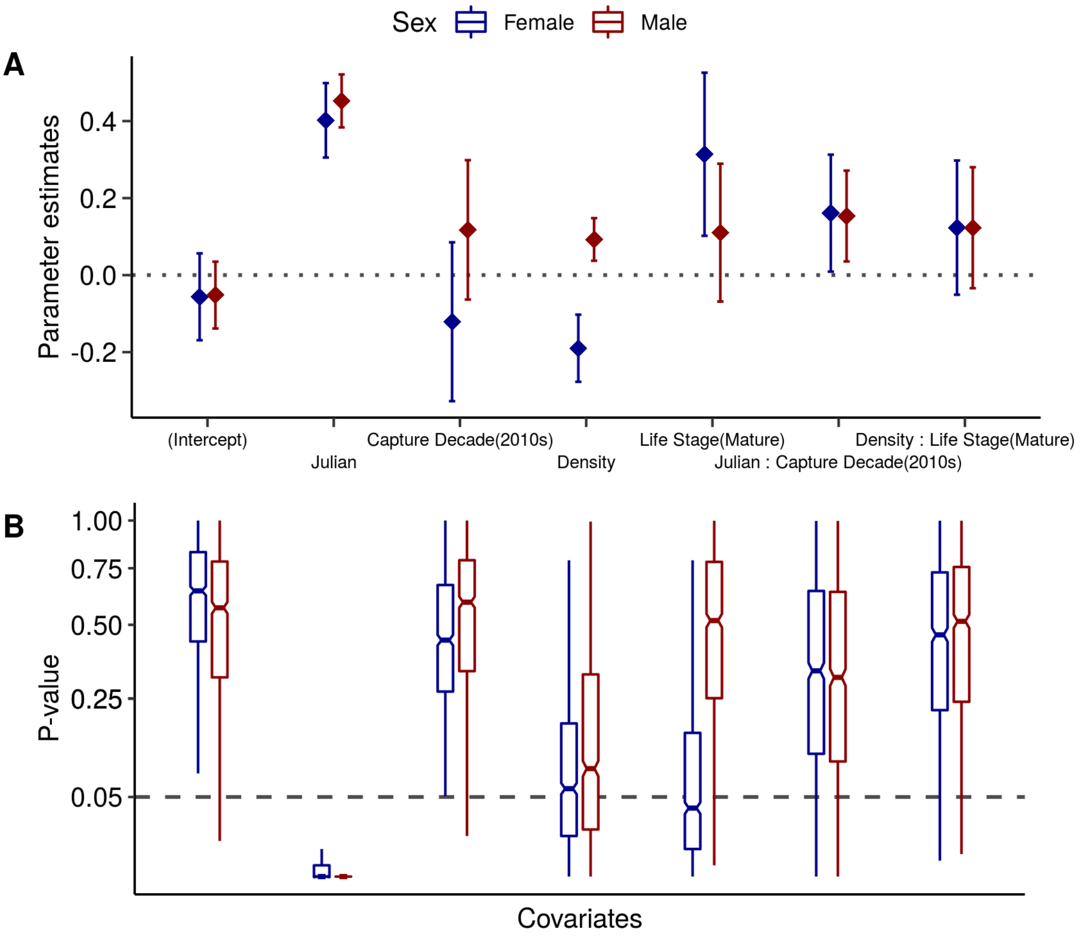

Figure S9.2 – A: Bootstrapped regression coefficients (mean ± 1 SD) of the fitted full model for predictions (iv) to (vi). B: P-value distributions of bootstrapped model's parameters for predictions (iv) to (vi). The dashed line marks the statistical significance level ($p = 0.05$) and the boxplot notch the 95% confidence interval of the median. The y-axis is scaled (by square root transformation) to highlight the values near the reference significance level.

General conclusion

We demonstrated that bears in the Alps, one of the world's most anthropized mountain regions, can coexist with humans by adapting their space use, movement, food source proximity, resting behavior, and energy expenditure. As humans are ecologically analogous to "super-predators" (Smith et al., 2017), the resulting interspecific competition has resulted in a modification of the fundamental and realized ecological niche for the brown bear, similar to the dynamics occurring in ecological communities (Chapron and Lopez-Bao, 2016). Additionally, human presence had a detrimental influence on bear mobility and landscape connectivity, preventing individuals from dispersing across the Eastern Alps and eventually establishing an Alpine-Dinaric metapopulation. Bears were only able to move across the landscape when human mobility was temporarily restricted (associated with the recent COVID-19 lockdown), and they did so by using previously identified but seldom used hot spots for road network crossing. These findings showed that, despite the ecological constraints imposed by humans, bears exhibited remarkable plasticity in responding to human-induced disturbance and presence on a daily basis, as well as adapting their mobility as conditions improved (and competition for space decreased).

This research has also resulted in the development of one of the first large-scale indexes of human cumulated outdoor activity, which is based on the world's largest freely viewable collection of GPS-tracked human outdoor activities (Strava, 2018). The COI, we suggest, was a first step toward the envisioned integrated science of movement (Miller et al., 2019) and an effort in converging research on animal movement ecology and human mobility science. Researchers have praised the newly-developed index for its ease of development and utilization and its ability to provide spatially explicit information about human presence in the landscape. Given the prevalence of recreational activities worldwide and the widespread availability of personal tracking devices, we believe that the COI may be implemented in all environments where it is assumed that the human effect on animals, and ecosystems in general, is not negligible.

The Alpine brown bear population is frequently cited as a success story in conservation since it was rescued from biological extinction (just three non-reproductive animals remained) through an outstanding concerted management effort. Over the span of two decades, the population has grown from the initial 10 released individuals to over 90, more than double the estimated minimum viable population (MVP) (Groff et al., 2020). Despite this impressive recovery, the population has not expanded significantly beyond the initial release range, owing to human-induced competition for space and barriers (Kaczensky et al., 2012; Peters et al., 2015). The predictive maps based on models fitted to brown bear movement data indicated that regions of high human activity (as expressed by the COI) were equally avoided when forecasting suitable areas for resting (Figure 3, Chapter 2) and within the home range (Figure 2, Chapter 1). In these areas of low probability of use, the active presence of humans in the landscape created 'non-physical' (i.e., psychological) barriers that animals struggled to overcome over the years, in addition to physical barriers. Only a temporary reduction in human mobility as a result of restrictions imposed to contain the COVID-19 outbreak showed that animals, if undisturbed, were able to cross these areas more often and overcome those barriers. Furthermore, those occurrences were largely reported in areas which both predictive maps indicate as unsuitable for bears. Human-dominated spaces, notwithstanding their unsuitability for bears, would have to be overcome in order to achieve long-term population expansion. Increased human competitive abilities (*sensu* Chapron and Lopez-Bao, 2016), together with a decline in acceptance of bears among local residents, could undermine the encouraging conservation results achieved thus far. Our research, in keeping with the hard work done thus far by institutions, examined the status quo, identified current key challenges, and proposed ameliorating actions. We were particularly interested in gathering evidence that could be utilized to improve future conservation efforts through active adaptive management (McCarthy and Possingham, 2007). Our findings serve as a foundation for the creation of more comprehensive socio-ecological models, as new challenges to coexistence occur as a direct result of early success and population expansion.

In a diametrically opposed ecological system, that of the Greater Yellowstone Ecosystem, the grizzly bear population has grown and expanded largely unaffected by humans for decades, especially without the burden of space competition that anthropogenic landscapes impose. High-calorie food sources, on the other hand, have declined as a result of environmental perturbations and species composition changes induced by humans. Despite these limitations, grizzly bears have demonstrated remarkable resilience by adapting their feeding tactics in response to increased population density, while also changes in food availability and accessibility occurred. This allowed grizzly bears to retain relatively high levels of individual performance despite density-dependent constraints. This was an important result compared to previous findings in the Alps, where we found multiple instances of the human-super predator outcompeting bears so as to make density-dependent effects likely less significant as compared to human-caused mortality. However, as the grizzly bear population inhabiting the Greater Yellowstone Ecosystem (i.e., "land-sparing") expands beyond the ecosystem's boundaries (i.e., "land-sharing"), unprecedented challenges and new human-bear conflicts akin to those in Europe will emerge. The Yellowstone

National Park has served as a world-class model of conservation for decades, but as large carnivores expand beyond the area of protection, new conservation models will be required, and the European experience (Chapron et al., 2012) could help inform decision-making in the years ahead. Allowing people and bears to coexist in the same landscape is a challenging task that will necessitate each adapting to the other's presence; this effort will be critical, now more than ever, for the long-term survival of bears as well as the ecosystems in which they thrive.

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Data derived from the Strava Global Heatmap has been used for non-commercial, research-only purposes. Less than 0.001% of the freely-viewable data were used according to the "Fair Use" statement (Section 107 of the Copyright Act of the United States of America) as well as is in compliance with articles 3 (“Text and data mining for the purposes of scientific research”) and 4 (“Exception or limitation for text and data mining”) of the new Directive (EU) 2019/790 of the European Parliament and of the Council of 17 April 2019 on copyright and related rights in the Digital Single Market and amending Directives 96/9/EC and 2001/29/EC, to be implemented by the Member States by 7 June 2021.

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