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Rent a room in the Alps: winter den site preferences of native and reintroduced brown bears

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Abstract

The management and conservation of large carnivores is a challenging task because of their great spatial requirements and the hostility encountered in certain socio-political contexts. Particular fundamental requirements concern those species, such as brown bears (*Ursus arctos*), that need to hibernate in order to optimise the balance between energy acquisition and energy expenditure during winter. Thus, a thorough knowledge of bears' winter behaviour is critical to ensure a proper management and protection of this species. The aim of the present study was to assess the location and features of the hibernation sites of a bear population reintroduced in the Central-Eastern Alps (Italy). Sixty-five bear dens and 85 unused caves were located and described. Bears were found to select natural rock caves ($N = 64$) located in medium-high slope at an altitude between 520 and 1950 m a.s.l.. Caves usually were in poorly accessible areas with low human disturbance. In particular, the comparison between used and unused caves showed that three main factors drove the selection of hibernation sites by brown bear: (i) small entrance and suitable length of the cave, (ii) their location in wooded areas and (iii) high level of solar radiation and favourable internal micro-climatic conditions. Caves selected by bears showed significantly higher monthly temperatures from October to March (especially in October and November, when bears typically search for a suitable hibernation site) than caves that were not used despite their similar structural characteristics. No differences in cave selection were found between native and reintroduced bears, suggesting that cave selection was driven by objective cave characteristics, rather than by population-specific traditions. Lastly, among different age and sex classes, pregnant females were found to select caves with a greater total length, located in more hidden areas and with more solar radiation around the entrance. Brown bear cave selection seems therefore to be driven mainly by measures, exterior habitat features and inner temperature.

Keywords *Ursus arctos* · Central-eastern Alps · Den · Hibernation · Reintroduction

Introduction

The management and conservation of large carnivores is a challenging task, mainly because of their huge spatial requirements (Noss et al. 1996) and the hostility they sometimes arouse in certain socio-political contexts on account of conflicts with human activities (Breitenmoser 1998; Treves and Karanth 2003; Can et al. 2014; Bautista et al. 2017).

Many species of large carnivores suffered a strong decline caused by the loss and fragmentation of their primary habitats that resulted in a closer proximity to humans and, therefore, in a range of conflicts (Linnell et al. 2001). This is especially true in Central Europe, where landscapes have been deeply modified, thus becoming crowded and fragmented, and where the protection of suitable habitats often includes international administrative borders (Linnell et al. 2008; Bischof et al. 2016).

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Particularly. serious plights concern those species that adopt energy conservation strategies during periods of poor food availability or harsh climatic conditions, as they need to avoid human disturbance. Hibernation is generally considered an energy conservation strategy (Wang 1989; Geiser 2004). In order to optimise the trade-off between energy acquisition and energy expenditure, energy is allocated to growth and reproduction when a surplus of food is available, while it is allocated exclusively to survival when food availability is low (Canale and Henry 2010). Indeed, during hibernation, metabolic energy expenses are lower than those required when active. If exposed to human disturbance, hibernating animals may move away from the den with a high energetic cost (Linnell et al. 2000) and den abandonment often affects survival rate (Linnell et al. 2000) and reproduction success (Swenson et al. 1997) negatively.

Among large carnivores, brown bears (*Ursus arctos*) survive through periods of low food availability and low temperatures by accumulating energy in the form of body fat, then by entering a period of dormancy in which their metabolic expenditures are lowered and they can draw on the energy reserves stored. Consequently, winter hibernation is an important aspect of the life history of bears, and suitable dens contribute to reduce energy losses during this season (Lentz et al. 1983). Albrecht et al. (2017) argued that human persecution (Zedrosser et al. 2011; Wolf and Ripple 2017) contributed to the decline of brown bear in the Holocene. Even presently, human presence can be considered the main threat to this species on account of direct killings and indirect disturbance during winter hibernation. Therefore, bears are expected to prefer dens where energy losses are minimal, distant from sources of disturbance and well insulated, with ambient temperature close to body temperature, in order to mitigate the effects of cold weather (see, e.g. Lentz et al. 1983; Hayes and Pelton 1994). Selecting a den with a favourable microclimate is especially important for adult females, because during the hibernation, they may have additional energy costs relating to gestation and nursing of cubs (Lentz et al. 1983; Ballard et al. 1987; Thomson 1992).

In Europe, brown bears use a variety of dens, such as rock caves, rock shelters and refuges completely dug into the ground (see, e.g. Krofel et al. 2017). To establish their preferences in the selection of dens is important for bear conservation especially because wintering is essential for their biology, which is crucial for their reproductive success as well as for their individual performance and fitness. Knowing which areas are preferred for hibernation should allow for more specifically targeted protection policies.

An effort to improve conservation strategies is particularly important in the case of reintroduced bear populations, such as the one in the Central-Eastern Alps, whose minimum viable population size was reached recently (see Tosi et al. 2015 for further details). Reducing disturbance to bears in relevant areas during den selection and occupancy could help maintain a favourable reproductive performance and individual survival rate during the limiting season, thus increasing the chances of re-stabilisation of the reintroduced population.

Moreover, preferences in winter den selection could differ between native bears and reintroduced ones, since it is not unusual for mammals to transmit patterns that increase individual fitness and population success across generations, thus building population-specific traditions (Avgar et al. 2014). This is the case, for instance, of the traditional use of seasonal ranges by ungulates (e.g. barren-ground caribou, *Rangifer tarandus* (Cameron et al. 1986; Nicholson et al. 2016); pronghorn, *Antilocapra americana* (Barnowe-Meyera et al. 2013)) or the denning site fidelity reported for bats (Willis et al. 2003; Willis and Brigham 2004; and see Lewis 1995 for a review). The transmission and perpetuation of certain behaviours may hinge on the memory of experienced individuals and on the strength of natal and adult philopatry within the population: both patterns were found in European brown bear populations (Dahle et al. 2006; Zedrosser et al. 2007).

In this framework, five general, non-excluding hypotheses on bear den selection can be formulated. Expected results and supported references were summarised in Table 1.

(H1) When the selected den is a rock cave, bears shall prefer caves with a small entrance, suitable volumes and a hidden access (*shape and dimension hypothesis*; Petram et al. 2004; Krofel et al. 2017).

(H2) Bears select their dens in inaccessible areas with a low potential for human disturbance during hibernation (*low disturbance hypothesis*; Swenson et al. 1997; Linnell et al. 2000; Petram et al. 2004).

(H3) Bears select caves with a good insulation and solar exposure in order to reduce energy loss (*energy optimisation hypothesis*; Folk et al. 1976; Nelson et al. 1983).

(H4) Preferences in winter den selection are inherited and differ between native bears and reintroduced ones (*inherited den selection hypothesis*; Dahle et al. 2006; Zedrosser et al. 2007).

(H5) Pregnant females select caves with greater volumes located in more remote areas where energy loss is allegedly less than near the caves selected by bears of other age or sex classes (*reproductive status hypothesis*; Cotton and Harlow 1995; Fernández et al. 2012; López-Alfaro et al. 2013).

Materials and methods

Study area

The study was conducted in a 700-km^2-wide area of Brenta and Paganella Massif (46° 05′ N; 10° 50′ E), Trento Province, Central-Eastern Alps, Italy (Fig. 1). Elevation ranged from 190 to 3160 m a.s.l. (mean elevation, 1379 m a.s.l). Forty-four

Table 1 Dependent variable used and group of independent variables tested according to the five hypotheses formulated (see Table 1 for the list of variables included in each group and their description). Expected results and supported references were reported for each hypothesis

Hypothesis	Group of independent variables tested	Dependent variable	Expected results (support references)
(H1) Shape and dimension	A	D	Selection of caves with smaller entrances and larger rooms, having suitable volumes with hidden accesses (Petram et al. 2004; Krofel et al. 2017)
(H2) Low disturbance	B	D	Selection of caves in inaccessible areas and higher safety requirements (Swenson et al. 1997; Linnell et al. 2000; Petram et al. 2004)
(H3) Energy optimisation	C	D	Selection of caves better insulated and that absorb more solar energy to reduce the energy loss (Folk et al. 1976; Nelson et al. 1983)
(H4) Inherited cave selection	A, B, C	E	Different caves selection criteria used by native and reintroduced bears (Dahle et al. 2006; Zedrosser et al. 2007)
(H5) Reproductive status	A, B, C	F	Selection of caves with greater volumes, in more remote areas (fewer disturbances) and where the energy loss is more minimised made by pregnant females. (Cotton and Harlow 1995; Fernández et al. 2012; López-Alfaro et al. 2013)

percent of this area was in the Adamello Brenta Nature Park, the largest protected area in Trentino. According to the latest version of CORINE Land Cover dataset (Commission of the European Communities 2012), more than 50% of this area is forested (up to the tree line at about 2000 m). The most representative coniferous species are European spruce (*Picea abies*), European silver fir (*Abies alba*) and European larch (*Larix decidua*), while beech (*Fagus sylvatica*), downy oak (*Quercus pubescens*), manna ash (*Fraxinus ornus*) and hop hornbeam (*Ostria carpinifolia*) are the most widespread broad-leaved species.

Brown bear population in the central-eastern Alps

Until the seventeenth century, brown bears were abundant and widely distributed across the Southern Alps as well as in the large, dense forests of the Pre-Alps and the Po plain. The start of their decline coincided with the increase in deforestation resulting from the increase in agricultural and livestock activities, which took place at the end of the eighteenth century (Dupré et al. 2000). During the nineteenth century, the increase in human settlements in remote areas, and the direct persecution by farmers and hunters caused the extinction of the bear populations in the Western Italian Alps (see Tosi et al. 2015 for further details). Subsequently, brown bears also became extinct in most areas of the Central and Eastern Italian Alps, with only three non-reproducing individuals surviving in the eastern range of the Brenta Mountains (the population was biologically extinct since 1989) (Castelli 1935; Daldoss 1976; Oriani 1991; Dupré et al. 2000; Mustoni et al. 2003).

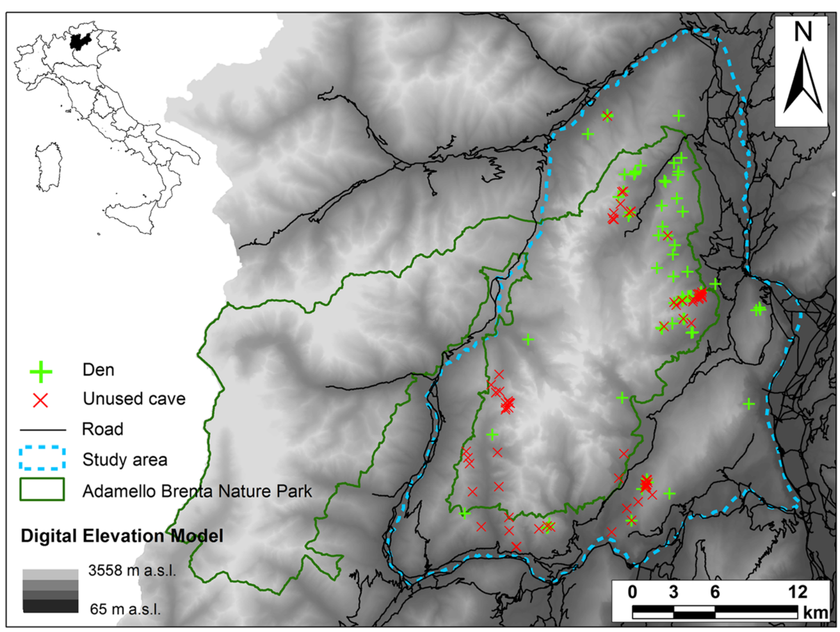

Fig. 1 Locations of bear dens ($N = 65$) and unused caves ($N = 85$) in a 703.16-km^2-wide study area on the Brenta and Paganella Massif (46° 05′ N; 10° 50′ E; Trento Province, Central-Eastern Alps, Italy) with a mean elevation of 1379 m (from 190 to 3160 m a.s.l.)

In an effort to reintroduce and preserve brown bears, Adamello Brenta Nature Park (Trentino, Italy) promoted a reintroduction project (*Life Ursus Project*, period: 1996–2004). The project aimed at restoring a minimum vital population (40–60 individuals, Dupré et al. 2000) in the Southern Alps in the mid-long term. To that purpose, 10 bears (7 females and 3 males) were translocated during 1999–2002 from a genetically similar population in Slovenia into the areas where the presence of non-reproducing individuals was still documented (Mustoni et al. 2003; Preatoni et al. 2005; Tosi et al. 2015). At the end of 2017, the reintroduced population counted 52–63 individuals (Groff et al. 2018).

Collecting data

Our study area was selected on the basis of (i) data available in literature about killing, hunting and sighting of bears over the winter seasons of the past century (Ambrosi 1886; Ramponi 1928; Castelli 1935; Daldoss 1981; Caliari et al. 1996; Groff et al. 1998); (ii) interviews to people who either knew the location of hibernation and bedding sites or had made direct observations in the period immediately before or after the hibernation period (Caliari et al. 1996); (iii) telemetry data from 10 reintroduced bears (see Tosi et al. 2015 for further details) and—after the reintroduction project—from 6 more bears collared or re-collared for management purposes; (iv) direct sightings, tracks, faeces and other indirect records (see Tosi et al. 2015 for further details).

A preliminary assessment of the selected study area was carried out to identify locations whose geomorphology could be compatible with the presence of bears' dens and to plan the on-field survey of the whole study area with the aid of 10 × 42 binoculars (Swarovski SLC-WB) and 60 × 80 telescopes (Swarovski ATS-80-HD), as well as topographic maps and photographic documentation.

The caves used by both native and reintroduced brown bears were identified by the presence of any nest or litter, excavation or additional indications such as bear scratches and hair. We recorded width and height of the entrance, total length, maximum and minimum width as well as maximum and minimum height of the cave (see Online Resource 1 for an example of description of den size). Caves where there was no sign of bear presence but whose structural parameters were within the range of those of the caves used as winter dens were classified as unused caves (e.g. Mysterud 1983; Servheen and Klaver 1983; Camarra 1987; Zunino 1988; Petram et al. 2004).

We also documented the characteristics of each bedding site within each cave (round or oval shape of the nest, litter, digging of the rest site) and each nest whenever available and intact (diameter, nest thickness, height of the cave above the centre; see Online Resource 2 for further details). Elevation and solar radiation were recorded at the entrance of both used and unused caves. Moreover, other variables (i.e. aspect, slope and habitat) were recorded on two different spatial scales: the cave itself and the general terrain inside a buffer of 100 m around it. Environmental descriptions of the caves were obtained from direct survey, while descriptions for the broader spatial scale (i.e. a buffer of 100 m) were obtained with the latest version of CORINE Land Cover dataset (Commission of the European Communities 2012) and the Digital Elevation Model (resolution at 10 m). Distance from paved and unpaved roads, urban areas, livestock sheds and mountain huts were calculated with technical maps of the Province of Trento and ortophotomaps (1994, 2006). All environmental data were derived using ArcGIS 9.3 (ESRI 2008).

In 70 unused and 63 used caves, microclimate characteristics were recorded six times a day with temperature data loggers (I-button®, DS1923 Hygrochron Temperature and Humidity Logger iButton with 8kB Data Log Memory; software I-Button-Viewer 32bit One-WireViewer.html) from 1 October to 30 April. Each data logger was arranged 20 cm above the centre of the bedding site (if present) inside a small net held by a nail (see Online Resource 3 for further details). In unused caves, data loggers were arranged in the most sheltered area of the cave. Thus, we were able to monitor the temperature of both used and unused caves over the whole hibernation period. Data collected by temperature loggers placed in caves occupied or visited by bears or other species during the survey period were eventually excluded from the analysis as the presence of animals was bound to alter ambient temperature.

Data analysis

General linear models (GLM, family = binomial) were fitted with R software version 3.1.0 (R Core team 2015) to assess the differences between (i) used vs unused caves; (ii) caves chosen by native bears vs those chosen by reintroduced bears and (iii) caves chosen by pregnant females vs those chosen by other age or sex classes. Models were fitted with all the biologically meaningful combinations of predictors reported in Table 2 according to the hypothesis being tested (see Table 1). We used the Information-Theoretic (IT) approach based on Akaike information criterion corrected (AICc) for small sample sizes (Burnham and Anderson 2002; Symonds and Mousalli 2011) to select the best fitting set of models. We looked at the variance inflation factors (VIFs) of all selected models, dropping any model with VIFs greater than 3 (threshold suggested by Zuur et al. 2010). The final set of models obtained was refitted by using the restricted maximum likelihood REML estimation and validated by checking the assumptions of normality, homoscedasticity and independence with the inspection of the standardised residual plots (Zuur et al. 2009). Akaike weight w_i for each i model was computed. The effect of each variable (i.e. parameter

Table 2 List of independent (A–C groups) and dependent (D–F groups) variables selected to test each hypothesis reported in Table 1. All the variables were measured or calculated for each cave discovered during the 2005–2011 fieldwork or available in Caliari et al. 1996

Group	Name [unit of measurement]	Independent (I) or dependent (D)	Reference scale	Description	Data availability
A - cave shape and dimension	Width [m]	D	Entrance	Size parameters	Direct survey
	Height [m]	D	Entrance		
	Max width [m]	D	Inside		
	Min width [m]	D	Inside		
	Total length [m]	D	Inside		
	Max height [m]	D	Inside		
	Min height [m]	D	Inside		
B - Disturbance	Elevation [m a.s.l.]	D	Entrance	Elevation of cave	Digital Elevation model of Trento Province (10 m resolution)
	Slope [degrees]	D D	Entrance Buffer 100 m	Slope of cave	Digital elevation model of Trento Province (10 m resolution)
	Dirt track [m]	D	Distance	Linear distance from the nearest source of disturbance	Technical maps of Trento Province (CTP 1:10000) and ortophotomaps (1994, 2006)
	Road [m]	D	Distance		
	Urban area [m]	D	Distance		
	Livestock shed [m]	D	Distance		
	Mountain hut[a] [m]	D	Distance		
	Habitat (open/closed)	D	Entrance	Open areas (0) vs Woodlands (1)	CORINE Land Cover dataset (Commission of the European Communities 2012)
	Forest [%]	D	Buffer 100 m	% of forest land use	
C – Energy	Aspect [degrees]	D D	Entrance Buffer 100 m	Aspect of cave	Digital elevation model of Trento Province (10 m resolution)
	Solar radiation[b] [kWh/m^2]	D	Entrance	Solar radiation during hibernation period	Digital elevation model of Trento Province (10 m resolution)
	Monthly temperature [°C]	D D D D	Mean Min Max Range	Monthly average temperature from October to April (see Fig. 2 for major details, here total October–April period was reported)	Temperature data logger (I-button®, DS1923 (6 measurements/day)
D – Utilisation	Utilisation	I	Dummy variable: used (1; $N = 64$[c]) vs unused (0; $N = 85$) caves		Telemetry data, direct sightings, tracks, faeces and other indirect records
E – Population	Population	I	Dummy variable: dens used by reintroduced (1; $N = 25$) vs native (0; $N = 39$) bears		Telemetry data, direct sightings, tracks, faeces and other indirect records
F – Reproductive status	Reproductive status	I	Dummy variable: dens used by pregnant females (1; $N = 10$) vs other age or sex classes (0; $N = 22$)		Telemetry data, direct sightings, tracks, faeces and other indirect records

[a] We refer to refuges for people in mountain areas (sky/tracking tourism)

[b] Solar radiation was calculated with Solar Radiation Tools in Spatial Analyst Toolset (Spatial Analyst extension for ArcGIS 9.3, ESRI 2008)

[c] The only den excavated in the roots of a tree was excluded from the analysis

estimation) included in a confidence set of models with ΔAICc ≤ 2 was obtained via model averaging in an AICc framework (model.avg.() function in MuMin packge for R; Burnham and Anderson 2002; Symonds and Mousalli 2011; Barton 2015).

We tested the variation in the size of entrances and the monthly variation in temperature between used and unused caves over each month of the hibernation period through a paired *t* test. Statistical analyses were performed with R version 3.1.0 (R Development CoreTeam 2015).

Results

Out of the 65 bear dens identified in the study area, 64 were natural rock caves. In one case only, the bear's winter recovery was a den dug among the roots of a spruce: this observation was excluded from the analysis. Other 85 unused caves were also documented (Fig. 1). Among the 64 used caves, 9 were occupied over the study period for a total of 20 hibernation events related to 14 collared bears.

Caves had small entrances and different inside volumes, and this variability was especially due to the total length of the cave (mean volume [width × length × height] = 2.0 × 5.9 × 0.9 m; see Online Resource 4 for a complete description of caves and Online Resource 1 for an example of collected measures). Among the different bedding types, bears preferred ground nests ($N = 44$, 67.7%), while litter ($N = 8$, 12.3%) and simple excavation ($N = 7$, 10.8%) were less common. In six cases (9.2%), the sole presence of vegetal residuals did not enable us to determine the bedding type. The vegetable material collected for the nests consisted in vegetation species (mainly herbaceous species, heather, leaves or branches) present within a short distance from the dens. Size was only recorded for intact nests ($N = 44$). Mean diameter of intact nests was 0.97 ± 0.33 m (see Online Resource 2 for further details).

Caves were located between 520 and 1950 m a.s.l. (mean ± SD = 1402 ± 277 m), mainly in sites with a south-eastern aspect and on a medium-high slope (see Online Resource 4 for further details), and usually in woodlands (81.3% vs 51.7% of available forest areas; specifically, 25.0% fir forest, 18.8% beech forest, 18.8% spruce forest, 15.6% coppice, 10.9% meadow, 4.7% scrub pine, 3.1% larch forest, 3.1% rock), far from possible sources of disturbance (i.e. urban areas and paved roads; see Online Resource 4 for further details).

The comparison between used and unused caves shows that bears selected their hibernation site according to three main drivers: (i) cave size (H1 verified), (ii) hidden habitat (H2 verified) and (iii) insulation of the cave and location in areas with higher solar radiation (H3 verified) (see Online Resource 5 for the set of models with ΔAICc ≤ 2 and Table 3 for parameter estimation of the average model).

Entrances of used caves were significantly smaller than the entrances of unused caves (height: $t_{147} = 2.935$, $p = 0.041$; width: $t_{147} = 3.123$, $p = 0.032$). The total length of the cave was also a crucial parameter, with bears preferring longer caves. Moreover, bears were found to prefer caves in forested areas. The average solar radiation recorded during the hibernation period at the entrance of the cave (dens = 376.7 kWh/m^2; unused caves = 287.7 kWh/m^2) was found to be a main driver, it being of a higher level in used caves (plus 31%). In addition, bears preferred caves with higher minimum inside temperatures throughout the winter period; used caves showed significantly higher monthly temperatures from October to March (Fig. 2). This difference was more pronounced in the months when bears selected their wintering areas (i.e. October [$t_{131} = 4.116$, $p < 0.001$] and November [$t_{131} = 3.260$, $p < 0.001$]), while no difference was recorded in April ($t_{131} = 1.311$, $p = 0.192$), when the hibernation period was over.

Out of a total of 64 caves, 39 were occupied by native and 25 by reintroduced bears. The translocated bears and their descendants chose caves in areas with the same characteristics as native bears (H4 not verified). Differences occurred only between the sizes of the entrances with reintroduced bears choosing caves with a lower height and higher width (see Online Resource 5 for the set of models with ΔAICc ≤ 2 and Table 3 for parameter estimation of average model).

Ten caves were occupied by pregnant females and 22 by either males or non pregnant females. The remaining 32 cases were excluded from this analysis as it was not possible to know the age or class of the individual which occupied the cave. Differences occurred with regard to the total length, with pregnant females choosing longer caves. Moreover, females gave birth in caves located in hidden areas (i.e. with the entrance covered by trees or shrubs) and with higher solar radiation (H5 verified; see Online Resource 5 for the set of models with ΔAICc ≤ 2 and Table 3 for parameter estimation of average model).

Discussion

In the Central-Eastern Alps, bears selected mostly natural rock caves for hibernating, consistently with other European populations (Linnell et al. 2000; Krofel et al. 2017). The selected caves, whose spatial distribution reflected the space use and the abundance/distribution of the last native bears and the reintroduced animals, had small entrances and large rooms and were preferably located in areas with little human disturbance and on south-facing slopes, where solar radiation helps limiting energy loss during hibernation.

The finding may be explained by the high availability of such shelters in the Brenta and Paganella Massif (as revealed by Huber and Roth (1997) in Dinara Mountains that showed a similar rock composition, i.e. calcareous rocks). However, data collection methods and the limited permanence over time of excavated dens may have favoured the discovery of natural rock caves over less resilient types of dens. Nests were found in most of the caves. This type of bedding probably provides a better insulation from the ground and, therefore, more comfortable thermic conditions during the winter months. According to Daldoss (1981), pregnant females and mothers with cubs born during the previous winter generally prepare larger nests with abundant vegetal material. In our dataset, in fact, a particular abundance of vegetal material was found in four caves used by pregnant females. In addition, Couturier (1954) assumed that the use of excavated beddings is limited to emergency conditions, when the former den must be abandoned on account of some disturbance and the bear does not have enough time for the preparation of a new nest. Moreover,

Table 3 Parameter estimates, standard errors, and 95% confidence intervals (CIs) of the best models explaining the variations (a) between used (1) and unused caves (0); (b) between dens used by reintroduced (1) vs native (0) bears; (c) between dens used by pregnant females (1) and other age or sex classes (0) in Brenta and Paganella Massif (Trento Province, Central-Eastern Alps, Italy). See Tables 1 and 2 for a complete description of the variables and hypotheses being tested

	CIs					
Parameter	ß	SE	Lower	Upper	*z* value	*p*
(a) Between used (1) and unused caves (0)						
Intercept	− 1.335	0.514	− 2.342	− 0.328	2.552	0.011
$\text{Width}_{(\text{entrance})}$	− 1.337	0.228	− 1.784	− 0.89	1.466	0.014
$\text{Height}_{(\text{entrance})}$	− 1.544	0.333	− 2.197	− 0.891	1.619	0.011
$\text{Maximum width}_{(\text{inside})}$	− 0.317	0.209	− 0.727	0.093	1.052	0.133
$\text{Total length}_{(\text{inside})}$	0.623	0.311	0.013	1.233	1.972	0.048
$\text{Maximum height}_{(\text{inside})}$	− 0.394	0.281	− 0.945	0.157	1.393	0.164
Elevation	− 0.236	0.244	− 0.714	0.242	0.958	0.338
$\text{Habitat}_{(\text{open vs closed})}$	1.143	0.536	0.092	2.194	2.115	0.034
$\text{Solar radiation}_{(\text{entrance})}$	0.778	0.222	0.343	1.213	3.473	<0.001
$\text{Minimum temperature}_{(\text{October})}$	1.502	0.293	0.928	2.076	2.202	0.015
(b) Between dens used by reintroduced (1) vs native (0) bears						
Intercept	− 0.327	0.643	− 1.586	0.934	0.502	0.616
$\text{Width}_{(\text{entrance})}$	1.302	0.696	− 0.062	2.666	1.833	0.067
$\text{Height}_{(\text{entrance})}$	− 1.229	0.597	− 0.059	− 2.399	2.018	0.044
$\text{Maximum width}_{(\text{inside})}$	− 0.403	0.440	− 1.265	0.459	0.896	0.370
Elevation	0.329	0.341	− 0.339	0.997	0.946	0.344
$\text{Habitat}_{(\text{open vs closed})}$	− 1.048	0.827	− 2.669	0.573	1.241	0.215
$\text{Solar radiation}_{(\text{entrance})}$	− 0.513	0.304	− 1.109	0.083	1.650	0.099
(c) Between dens used by 627 pregnant females (1) and other age or sex classes (0)						
Intercept	− 0.829	0.489	− 1.787	0.129	0.502	0.021
$\text{Total length}_{(\text{inside})}$	1.022	0.473	0.095	1.949	0.946	0.048
Elevation	− 0.577	0.632	− 1.816	0.662	1.65	0.087
$\text{Habitat}_{(\text{open vs closed})}$	1.128	0.375	0.393	1.863	2.018	0.011
$\text{Solar radiation}_{(\text{entrance})}$	1.302	0.541	0.242	2.362	2.143	0.002
$\text{Minimum temperature}_{(\text{October})}$	0.347	0.381	− 0.400	1.094	0.748	0.334

Average model (used vs unused caves): $\Delta\text{AICc} \leq 2$; $R^2 = 0.52$

Average model (reintroduced vs native bears): $\Delta\text{AIC} \leq 2$; $R^2 = 0.20$

Average model (pregnant females vs other age or sex classes): $\Delta\text{AIC} \leq 2$; $R^2 = 0.29$

the bedding materials, mainly represented by herbaceous species, heather, leaves and branches, usually corresponded to those available in close proximity of dens (see also Clevenger et al. 1992), thus indicating that bears select caves regardless of the vegetation types around.

The most uniform values among all size parameters were those of the entrances, which were particularly small. These measures, especially the height, are comparable to those found in other studies carried out in France (average height of 0.87 m—Camarra 1987) and in Slovenia (average height of 0.59 m and 0.62 m in Petram et al. (2004) and Krofel et al. (2017), respectively). This size range may be preferred by bears by virtue of the greater protection provided by snowfall closing the entrance and the consequently reduced visibility and disturbance (Caliari et al. 1996). As reported by Petram et al. (2004), cave length was another important factor, with an average of 3.94 m for dens. In our study area, the total length of caves was even higher (5.9 m on average). As predicted, all the preferences observed may be accounted for by the bears' inclination to select caves with small entrances and large rooms.

Brown bears chose their hibernation sites in medium elevation range, usually under the tree line (about 2000 m a.s.l.) and medium-high slope which are areas sheltered from human disturbance, as reported in other European studies (Camarra 1987; Clevenger et al. 1992; Petram et al. 2004; Elfström et al. 2008; Elfström and Swenson 2009; Sahlén et al. 2011). However, ursids in general and brown bears outside Southern Europe showed great variability in den site selection (see Linnell et al. 2000 for a review), which confirms the importance of local studies to better prepare and develop conservation and management plans. Moreover, bears hibernated in caves located far from human infrastructures (Tietje and Ruff 1980; Johnson and Pelton 1981; Schoen et al. 1987; McLellan and Shackleton 1989; Petram et al. 2004). The average distance from unpaved roads and livestock shelters,

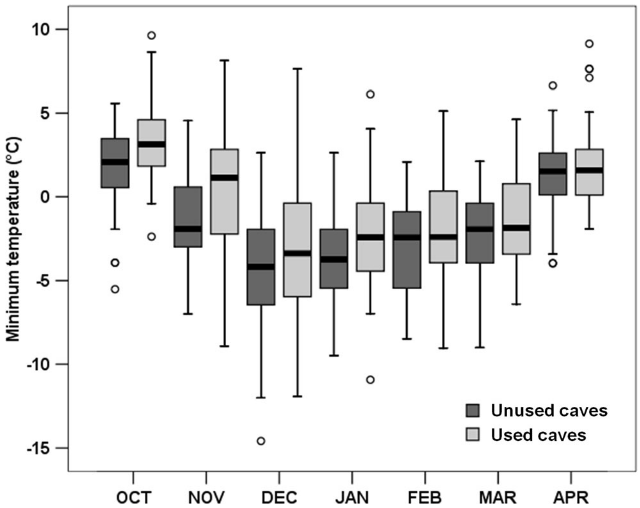

Fig. 2 Differences in monthly minimum temperature recorded in unused (in black; $N = 70$) and used caves (in grey; $N = 63$). Temperature loggers were not placed in all the bedding sites. Caves that were occupied or visited by bears or other species during the survey period were excluded from the analysis

instead, was not significant, which suggests that this type of infrastructures does not affect the selection of hibernation sites negatively, possibly because in our study site the viability of unpaved roads in autumn and even more so in winter is particularly limited, thus reducing the occasions of human disturbance. Even the distance from urban areas and mountain huts was not included in the best models, possibly because in our study site the average distance of available caves from these kinds of human disturbance is high, bearing bears to spend winter in quiet and safe places. Thus, as Petram et al. (2004) reported, bears generally select inaccessible areas with a low potential for human disturbance.

Hibernating in hidden and safe areas concurs with the selection of thermic conditions inside and outside the caves to optimise the bears' energetic balance (Folk et al. 1976; Nelson et al. 1983). Our data revealed a prevailing south-eastern aspect of both the caves' entrance and the mountain side. A similar pattern was reported in Spain (Clevenger et al. 1992), while in the French Pyrenees and in Slovenia, no aspect was found to be clearly preferred (Camarra 1987; Krofel et al. 2017). In our dataset, the south-eastern aspect of both the cave's entrance and the mountain side is one of the key factors accounting for the high values of solar radiation recorded in the sites chosen by bears. The selection of caves that absorbed more solar energy and were better insulated ensured higher minimum inside temperatures throughout the winter period.

Reintroduced bears were found to choose caves according to the same criteria as native bears, thus confirming the optimal adaptation of the former to new environments (see Tosi et al. (2015) for further details on the outcomes of the reintroduction project) and suggesting that cave selection is not driven by population-specific transmission of traditional behaviours. However, significant differences revealed in cave entrance measures—with reintroduced bears choosing caves with lower height than native ones—could be related to the need to keep the suitable microclimate inside the cave in winter. Considering the ongoing snow cover trends (see Gobiet et al. (2014) for a review about snow cover trends on the Alps and Trento province official data (www.climatrentino.it) about local snow cover data), entrances with lower height can ensure a better insulation even in winters with little snowfall. At the same time, caves in hidden areas may be less subject to the disturbance caused by the increased mountain exploitation related to winter tourism (i.e. encounters with humans are less probable; see Petram et al. 2004). However, no significant difference was found as to the environmental conditions related to other kind of human disturbance, thus suggesting that the level of disturbance in wintering areas has not changed significantly over the last few decades. Indeed, in certain respects, the use of mountainous areas by man was even greater in the past than it is now (e.g. for pastoralism and agriculture activities; Trento province official data: www.statweb.provincia.tn.it).

Although bears are facultative hibernators (Cotton and Harlow 1995), the use of winter dens is essential for pregnant females to give birth (López-Alfaro et al. 2013) and their denning site selection showed particular characteristics if compared to that of other age or sex classes. Pregnant females were found to prefer caves with bigger volumes and hidden entrances to host their cubs and protect them in their first weeks of life. Moreover, higher levels of solar radiation could help the mothers' thermoregulation process during the hibernation period (i.e. during their gestation and nursing of cubs) as well as during the early post-hibernation interval, when cubs remain alone in the caves for short periods or when they start to attend areas around the entrance.

Conclusion

This study evaluated the selection of hibernation sites by a population of brown bears reintroduced into the Central-Eastern Alps (Italy). High energetic costs are related to den abandonment, affecting survival rate and reproduction success. Thus, to reduce the potential disturbance for the bears and the risk of surprise encounters between humans and bears, recreational, forestry and hunting activities should be either banned or minimised in areas close to rocky outcrops and along steep slopes in woodlands, during the hibernation period.

Moreover, our findings on the use of caves with increasingly smaller entrances call for careful consideration. These findings may be explained by the increase in winter recreational activities (i.e. a greater human attendance of areas far from urban environment), just as much as they could be an answer to the ongoing climate change (i.e. less stable thermic conditions in winter, with an increase in extreme events, and a negative snow cover trend in the last decades). In the study population, pregnant females were found to be the most demanding group as to the characteristics of the caves. Thus, the monitoring of hibernation sites, especially for this category, should be considered a valuable tool for planning a sustainable environmental development, but also an effective means to assess the impact of climatic change on mountainous systems.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval The study complies with all relevant national, regional and provincial Italian laws and with all ethical standards.

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