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Can landscape characteristics help explain the different trends of Cantabrian brown bear subpopulations?

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Abstract

A central challenge in animal conservation is to understand how a population may respond to different habitat characteristics, which may affect their growth and viability. At the beginning of the twentieth century, the Cantabrian brown bear *Ursus arctos* population (north-western Spain) was separated into western and eastern subpopulations. Today, brown bears in the Cantabrian Mountains are recovering and the two subpopulations are reconnected. However, the western portion of the population represents ca. 90% of the entire population, the number of females with cubs-of-the-year has also shown a more rapid increase in the western subpopulation than in the eastern one and mean litter size is significantly larger in the west. By comparing the characteristics of the landscape used by brown bears in the western vs. eastern sectors of the population, we intended highlighting focal elements of landscape composition and structure that may help explain the differences in numbers and fecundity of these two subpopulations. We suggest that habitat use alone might not have the expected role in potentially explaining differences between subpopulations. Both the current positive trend of the Cantabrian population and our results seem to show that the dynamics affecting these subpopulations might be more complex than previously believed and cannot be understood on the basis of habitat analyses only. Suspicions may arise around direct human influences (e.g. persistence of poaching and/or bad practices during hunting) on the different trends exhibited by the two sectors of this endangered bear population.

Keywords Habitat fragmentation · Habitat use · Human-modified landscapes · Human-dominated landscapes · *Ursus arctos*

Introduction

The size and intrinsic dynamics (e.g. fecundity and mortality) of animal populations may be related to different properties of the landscape, such as habitat quality, vegetation composition and fragmentation of key habitat patches, i.e. the size and isolation of habitat patches, as well as the amount of habitat available (Fahrig 2003; Pardini et al. 2005; Honorato et al. 2015). Indeed, habitat loss and fragmentation may also decrease the viability of animal populations because in small populations, the influence of stochastic processes may increase (Pardini et al. 2005; Penteriani et al. 2005a, 2005b, 2008). Thus, a central challenge in animal conservation and management is to understand how a population (or a subpopulation) may respond to different habitat characteristics, which may affect their growth and viability. To this end, habitat analyses at different scales may help provide complementary information, from individual requirements and their responses to local environmental variability to population patterns and processes (Martin et al. 2012).

Brown bears *Ursus arctos* inhabiting the Cantabrian Mountains (north-western Spain) represent the westernmost population of the species' range in Europe. Of the four isolated brown bear populations in western Europe, i.e. Italian Apennines and eastern Alps, Pyrenees (France and eastern Spain) and Cantabrian, the latter represents the only population showing a trend to natural recovery (Gonzalez et al.

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2016). At the beginning of the twentieth century, the Cantabrian brown bear population was separated into western and eastern subpopulations by a 50–100-km-wide strip of land, with bears in the two subpopulations declining in number until the mid-1990s (Palomero et al. 2007; Gonzalez et al. 2016). Today, brown bears in the Cantabrian Mountains are showing a positive trend and the two subpopulations are reconnected (Pérez et al. 2010; Gonzalez et al. 2016). However, the western portion of the population is considered to represent ca. 90% of the entire population, for which a genetic census conducted in 2006 estimated approximately 203 bears (confidence interval CI 95% = 168–260) in the west and only 19 bears (CI 95% = 12–40) in the east (Pérez et al. 2014). The number of females with cubs-of-the-year (FCOY), a proxy of the population trend, has also shown a more rapid increase in the western subpopulation than in the eastern one (6 vs. 34 FCOY in 2016 and an average of 4.3 vs. 25 FCOY during the 10-year period 2007–2016; unpublished data from Gobierno del Principado de Asturias, Junta de Castilla y León, Gobierno de Cantabria and Xunta de Galicia; (Palomero et al. 2007). Mean litter size is 1.8 ± 0.2 cubs ($n = 596$ cubs) in the west and 1.3 ± 0.6 cubs ($n = 99$ cubs) in the east, with the former being significantly larger than the latter (Mann-Whitney test $Z = -4.66$, $P = 0.0001$, $n = 29, 27$) (Penteriani et al. 2018). Thus, despite the consistent positive trend in population size of the western subpopulation of Cantabrian brown bears, the eastern subpopulation has had a substantially smaller population increase (Martínez Cano et al. 2016). Such trends have characterised these two populations over the last 40 years (Palomero et al. 2007; FAPAS/FIEP 2017).

The contrast in population growth between the western and eastern subpopulations might suggest high mortality rates in the eastern subpopulation and/or a relatively limited dispersal of bears out of the western sector. Indeed, some previous studies have suggested the following: (1) that the western sector is a zone of high human impact but with good habitat quality, whereas the eastern zone shows low human impact but suboptimal bear habitats (Wiegand et al. 1998); and (2) a narrow connection between the two subpopulations, apparently a consequence of the development of communication infrastructures (García et al. 2007; Pérez et al. 2010; San Miguel et al. 2012; Mateo-Sánchez et al. 2014b). However, even if female philopatry has been highlighted as one of the causes of the slow rate of recolonization of the eastern sector (Palomero et al. 2007), this cannot explain the apparent lower reproductive rates or higher mortality in this subpopulation, which is clearly exhibiting a slower increase than the western subpopulation. Earlier studies have also indicated (3) that the principal mechanism determining changes in FCOY is the effect of environmental factors (e.g. resources availability) on mortality rates, as individual-based modelling seems to point out (Martínez Cano et al. 2016); and (4) a prevalence of low quality food-items in the eastern sector of the Cantabrian Mountains (Clevenger et al. 1992; Naves et al. 2003, 2006). For example, during the hyperphagic season, eastern bears consume a high proportion of less energetic foods (e.g. graminoids and forbs), which may engender a lower accumulation of fat and, consequently, could restrict the duration of hibernation and result in less reproductive success than the western subpopulation (Naves et al. 2006).

Here, we compared the characteristics of the landscape used by Cantabrian brown bears in the western vs. eastern sectors of the population, with the main aim of highlighting focal elements of landscape composition and structure that may help explain the above-cited differences in numbers and fecundity of these two bear subpopulations. A better knowledge of the habitat used by individuals of both these subpopulations can offer crucial insights for the conservation and management of this small, isolated and endangered brown bear population at the limit of the species' occidental range.

Methods

Study area Our habitat analyses encompassed most of the Cantabrian range currently occupied by brown bears (Asturias, León and Palencia provinces). The Cantabrian Mountains are one of the main mountain range systems in Spain, stretching over 300 km across the northern part of the country, running east-west parallel to the Atlantic coast. Maximum elevation is 2648 m a.s.l. and average elevation is around 1100 m (Martínez Cano et al. 2016). As a general rule, the eastern sector of the Cantabrian Mountains is characterised by higher average altitudes (1300 m a.s.l.) and lower average slopes (21%) than the western area (700 m a.s.l. and 34%) (Naves et al. 2003). The Cantabrian Mountains are characterized by an oceanic climate, with pronounced differences on opposite slopes of the mountain range (Pato and Obeso 2012; Mateo-Sánchez et al. 2014b; Roces-Díaz et al. 2014): northern slopes exhibit mild winters and rainy summers, with fewer days of frost and less snow accumulation in winter, while on southern slopes, winters are longer and colder, with ample snow and fresh and short summers without drought. The greater thermal amplitude and lower rainfall is accentuated towards the east due to the higher average altitude of the range. More specifically, average rainfall ranges from more than 900 mm per year in the lowest zones to more than 2000 mm at the highest elevations in the west; due to the Foehn effect, rainfall drops to 700 mm per year in some areas of the eastern sector.

Subalpine matorral (*Juniperus communis*, *Vaccinium uliginosum*, *V. myrtillus* and *Arctostaphylos uva-ursi*) dominates mountain areas above the treeline (~ 1700 m) (Martínez Cano et al. 2016). Sites below 1500 m a.s.l. mainly consist of deciduous forests of oak *Quercus petraea*, beech *Fagus sylvatica* and chestnut *Castanea sativa*, with bilberry dominating the understory (Pato and Obeso 2012). In some areas, former forests have been converted into pasture and brushwood (*Genista*, *Cytisus*, *Erica* and *Calluna*) through human activities (Naves et al. 2003, 2006).

Throughout the entire study area, bears are surrounded by a matrix of urbanised and cultivated areas, with a high density of transport routes (Mateo-Sánchez et al. 2016). There are differences between the areas occupied by humans in both bear subpopulations, with an average population density of 4.9 inhabitants km^{-1} in the municipalities occupied by the eastern subpopulation and more than double that figure (10.9 inhabitants km^{-1}) in the western area (INE 2017). Throughout the study area, the main economic activity is the extensive breeding of livestock, particularly cattle, followed by mining and tourism, as well as other activities such as hunting and timber harvest (Fernández-Gil et al. 2006). Cattle density (bovine, equine, ovine and caprine), equated to 'heads of adult cattle' (UGM), does not differ substantially between the municipalities where both bear subpopulations are located (18.5 UGM km^{-1} in the eastern area and 15.6 UGM km $^{-1}$ in the western one) (1131/2010 RD 2010).

Brown bear data The locations of brown bears were obtained from (1) direct bear observations that were georeferenced by personnel of the Principado de Asturias and Junta de Castilla y León, primarily by the Patrulla Oso, i.e. the Bear Patrol, of the Principado de Asturias and of the Junta de Castilla y León, as well as by all the other guards of both regional governments, by the Asturian Foundation for the Conservation of Wildlife (FAPAS, Fondo para la Protección de los Animales Salvajes), the FOA (Fundación Oso de Asturias) and the Brown Bear Foundation (FOP, Fundación Oso Pardo); (2) remotely triggered cameras that were randomly placed by the FAPAS and Bear Team during the last **20** years, mainly in forested areas where bears are less visible (FAPAS/FIEP 2017) and (3) personal georeferenced observations of the authors. Thus, the long-term monitoring of the Cantabrian population, which started at the beginning of the **1990s**, is essentially based on direct sightings (i.e. direct observation and pictures obtained from camera traps) and the location of indirect signs of presence, i.e. footprints, fur and scats, as well as records of damage caused by bears to livestock, beehives, crops and human activities and infrastructures. Consequently, locations were both the result of systematic observations and random observations. For the western sector of the Cantabrian Mountains**,** it was possible to collect 7194 bear locations (from 1992 to 2017), whereas for the eastern sector, 1541 bear locations were available (from 1985 to 2017; Fig. 1). We collected data following the guidelines of the American Society of Mammalogists (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016).

Landscape characterisation The delimitation of the bear subpopulations can be artificially represented by the A-66 highway from Oviedo to León (Fig. 1). In order to clearly distinguish the main habitat of the two subpopulations, brown bear locations within 3000 m of both sides of the highway were removed from the analyses. Moreover, because we had relatively few observations between 1985 and 2000 (5%) and the landscape characteristics might have been considerably different before 2000, we removed such observations from our analyses and only included the most recent data (2000–2017). The multi-scale approach to determining bear habitat use was based on four different spatial scales, i.e. circular plots with radii of 500, 1000, 2000 and 3000 m, respectively, around each bear location (see also Penteriani et al. in press). These plots covered most of the bear's movements in the study area (Clevenger and Purroy 1988; Penteriani et al. 2017). This approach is based on Johnson's (1980) model, which assumes that animals make decisions about basic resources (e.g. breeding sites, cover and food) at retrogressively smaller scales and in a hierarchical manner, ranging from local factors within habitat patches to broad scale determinants of home range selection and population distribution at landscape levels (Gastón et al. 2017). To understand relevant habitat patterns as perceived by animals in complex landscapes, it is necessary to identify the scales at which particular environmental variables influence habitat selection and, therefore, it is recommended that habitat modelling follows a multi-scale approach (Gastón et al. 2017). In fact, what may seem appropriate at one scale may have little importance at another, making the results dependent on the scale (Ciarniello et al. 2007). Indeed, habitat relationships are highly sensitive to the scale at which explanatory variables are assessed for brown bears in the Cantabrian Mountains (Mateo-Sánchez et al. 2014a).

The landscape characteristics of both brown bear subpopulations of the Cantabrian Mountains were characterized by three categories of variables: (1) landscape composition, (2) landscape structure (i.e. fragmentation), and (3) human footprint, i.e. landscape variables associated with humans. As to landscape composition, several variables were taken into account at the above-mentioned four spatial scales. The altitude of the plot centres (m a.s.l.) was obtained from an altitude raster layer of the Iberian Peninsula (http://www.diva-gis.org) and calculated by the QGIS software (QGIS Geographic Information System 2015) using the 'Point Sampling' tool. Ruggedness was determined from the total length (m) of the linear development of the elevation curves ($length function of the QGIS software). The same approach was applied to obtain river density. The landscape GIS layers extracted from the Centro de Descargas del CNIG (IGN; Cartografía Temática Ambiental of the Principado de Asturias; Hojas del Mapa de Vegetación, Litología, Roquedos y Hábitat del Oso. 2011. Escala 1:25000. © Principado de Asturias, Spain) were reclassified into eight

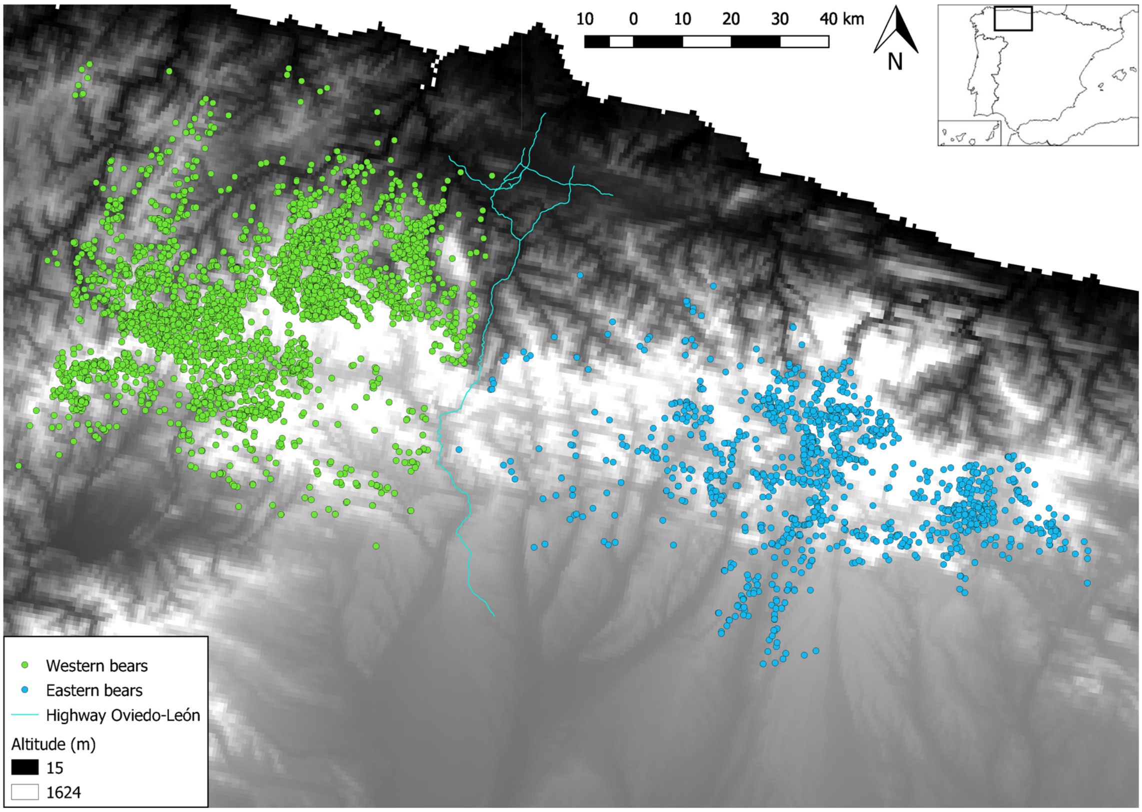

Fig. 1 Distribution of the brown bear locations (western vs. eastern subpopulations) in the Cantabrian Mountains (north-western Spain) used in this study

habitat types: (1) human settlements and infrastructures (which belong to the human footprint category) (2) crops, (3) fruit trees, (4) forest (i.e. hardwood and mixed forests), (5) conifer forests, (6) pasture, (7) shrubland, and (8) rocky areas. The Intersect tool was used to obtain the percentage of land use in each plot. This function extracts the information contained in the plots, and then the $area function determines the area (%) occupied by each habitat type in the different plots that we analysed.

Linear structures belonging to the human footprint category, such as road and trail densities, were analysed using the same $length function. In addition, the shortest distances from human infrastructures were calculated by using the Hub distance function.

Statistical analyses Statistical analyses only included those habitat parameters with less than 20% of zeros in all the buffers considered. The variables ‘conifer’ and ‘forest’ were highly correlated ($r = 0.85$) and, therefore, we excluded the variable ‘conifer’, which represents a lower quality habitat for bears than hardwood or mixed forests (Clevenger et al. 1997).

To explore possible differences in landscape characteristics between the two subpopulations, we built GLMMs with a binomial distribution which included the location of bears either to the east (0) or west (1) subpopulation as the response variable and the landscape parameters as predictor variables. Specifically, for each of the four spatial scales, we constructed a set of competing models that included all possible combinations of predictor variables, from the simplest null model (intercept model only) to a complete model that included all the landscape parameters.

The best competing model or set of models was chosen based on Akaike’s information criterion (AICc). Models with a ΔAICc below 2 were considered as equally competitive. Values of ΔAICc and weighted AICc, indicating the probability that the model selected was the best among the competing candidates (Table 1), were calculated as well. Parameter coefficients and the relative importance value (RIV) of each

Table 1 Values of AICc, ΔAICc and Weighted AICc of the best models or sets of models (ΔAICc < 2) for the four spatial scales at which potential differences of brown bear habitat use between the western and eastern sectors of the Cantabrian Mountains were analysed

	Selected models*	AICc	ΔAICc	Weighted AICc
500 m	1/2/3/4	4356.39	0	1
1000 m	1/2/3/4/5	3946.89	0	0.98
2000 m	1/3/4/5	3881.63	0	0.7
	1/2/3/4/5	3883.29	1.66	0.3
3000 m	1/2/3/4/5/6/7/8	3104.07	0	1

*1 = altitude; 2 = ruggedness; 3 = % forest; 4 = % shrubland; 5 = river length; 6 = road length; 7 = trail length; 8 = rocky areas explanatory variable were generated by employing model averaging on the 95% confidence set (Burnham and Anderson 2002). Models were run in R v. 3.5.1 statistical software (R Foundation for Statistical Computing 2018) using the lme4 package (Bates et al. 2015). Model generation and model averaging were performed using the MuMIn package (Bartoń 2013).

Furthermore, in order to characterize landscape structure in the western and eastern sectors, we created two raster files using QGIS software and the *LecoS* (Landscape ecology Statistics) tool (Jung 2016). This tool allows the overlay of a polygon and a raster in order to study the fragmentation of the landscape. The east and west sectors were defined with the external points of the bear locations. A polygon for each sector was therefore set in this way to overlay with the land cover raster. The following indexes were calculated for forest and shrubland classes in Fragstats software (McGarigal et al. 2012): edge density (ED; equal to the sum of the lengths (m) of all edge segments in the landscape, divided by the total landscape area (m^2), multiplied by 10,000 to facilitate the display of the results), largest patch ndex (LPI; at the class level quantifies the percentage of total landscape area comprised by the largest patch), mean patch size (MPS), mean nearest-neighbour distance (MNN; defined using simple Euclidean geometry as the mean shortest straight-line distance between the focal patch and its nearest neighbour of the same class) and number of patches (NP). At the landscape scale, Shannon (SHDI) and Simpson (SIDI) diversity indices were calculated.

Results

Our habitat analyses showed some relevant differences in the landscape composition and structure used by brown bears within each subpopulation (Fig. 2). At all scales, the best model always included altitude, ruggedness, percentage of forest and percentage of shrubland. At the 1000 and 2000 m scales, the best model also included river length. At the largest scale (3000 m), road length, trail length and rocky areas were also included in the best model together with all the abovementioned variables (Table 1). The importance of these variables in explaining the difference between the two subpopulations was also supported by their values of p, CI and RIV (Table 2). Specifically, at each spatial scale, western brown bears used areas characterised by higher values of ruggedness and shrubland than eastern bears, which are generally located at higher altitudes and in more forested areas (Table 2; see also SD1 and Fig. 2). At the largest spatial scale (3000 m), western bears used more rocky landscapes and inhabited areas characterised by a greater human footprint, i.e. areas with longer road and trail lengths, compared to eastern bears.

From a structural point of view (Table 3): (1) forest cover was found to be more fragmented in the western sector, as revealed by the larger number of patches as well as the lower values of largest patch index and mean patch size compared to the east; similarly, (2) shrubland also seemed to be more fragmented in the west, as demonstrated by the larger number of patches; (3) western and eastern sectors showed similar values for edge density, mean nearest-neighbour distance and landscape diversity (calculated by Shannon's and Simpson's indexes).

Discussion

The best models for brown bear habitat use in the Cantabrian Mountains were at all scales characterised by altitude, ruggedness and percentage of forest and shrubland, which have the potential to most effectively separate the western from eastern bear habitat use. As a consequence, if habitat use plays a role, at least partially, in determining the different trends observed in the two subpopulations, these four landscape descriptors might be the most important in explaining such dissimilarities. These variables may be even more relevant than the human footprint considered by our analyses, which was shown to be higher in the denser and more productive western subpopulation. And this, despite the fact that habitat suitability models seem to indicate that brown bears avoid human infrastructures and agricultural areas in the Cantabrian Mountains (Martin et al. 2012). This may suggest that human pressure in terms of infrastructures (road and trail lengths) may not be the factor limiting the growth of the eastern population. Indeed, the presence of roads and trails may have minimal influence on bear distribution as long as they do not represent impassable barriers (Mateo-Sánchez et al. 2015). However, when measuring only indirectly human footprint through proxies, these parameters do not necessarily represent the intensity of the pressure that man actually exerts on a territory. Thus, such a possibility might still be interpreted with caution and deserves further attention.

As also recently highlighted by Martínez Cano et al. (2016), higher fecundity and population size in the western sector might be explained in part by the habitat used by bears: (1) the western subpopulation inhabits a sector characterised by a greater availability in shelters, such as rocky or rugged areas, as also suggested by Mateo-Sánchez et al. 2014a, 2016). Indeed, in the Cantabrian Mountains, a human-modified landscape largely dominated by the presence of human infrastructures, rocky and rugged areas may allow bears to more easily avoid human presence and activities. Also, (2) shrubland, which is more frequently used by western brown bears, might provide an additional source of shelter and trophic resources. Because of the importance of habitat connectivity for brown bears in the Cantabrian Mountains (Mateo-Sánchez et al. 2014a), shrubland may also increase matrix

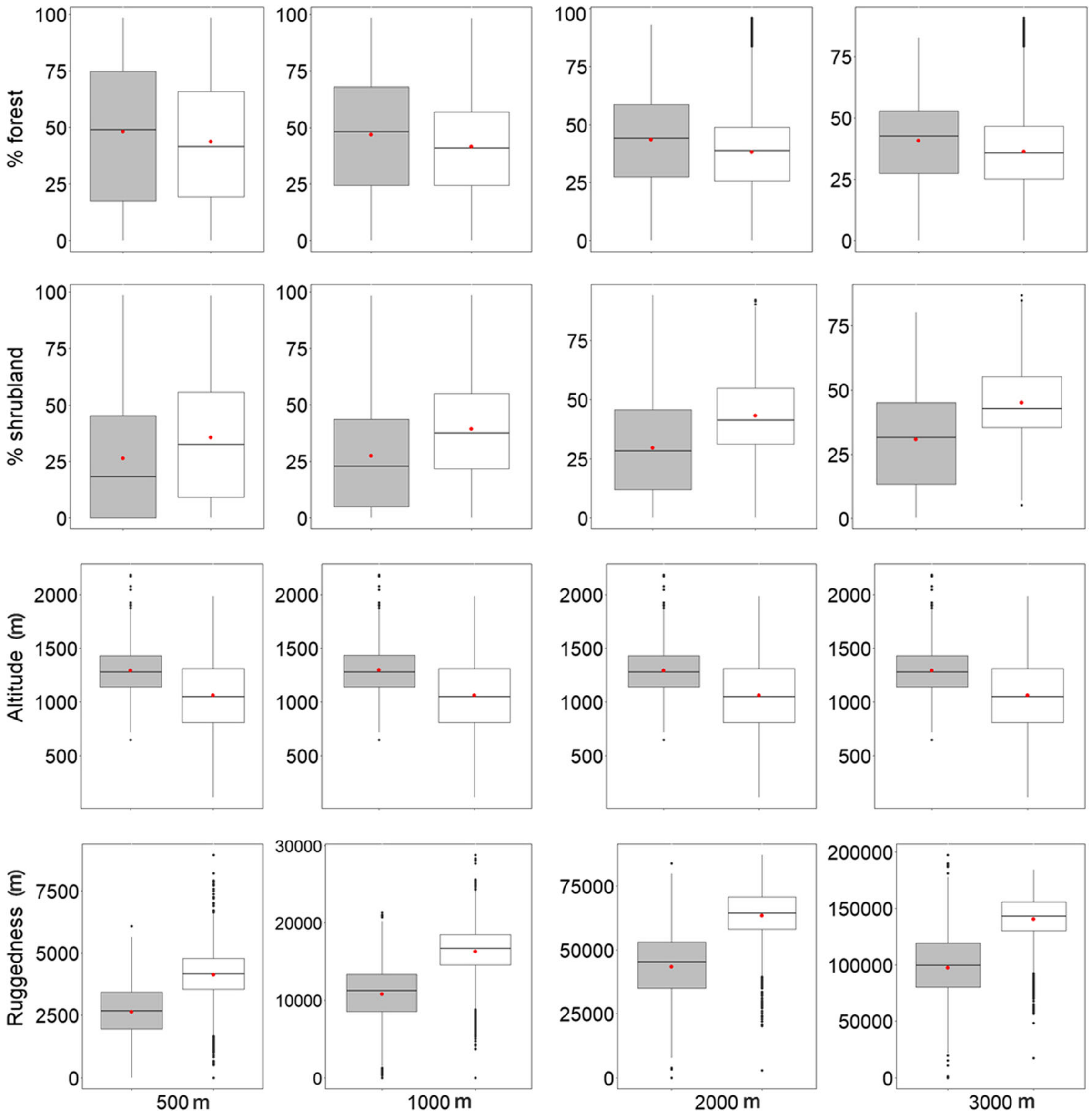

Fig. 2 Boxplots showing the median, mean (red dots) and range of the values of the habitat variables (see Table 1) that were included in the best models built to characterise the western (1) vs. eastern (0) brown bear habitat use in the Cantabrian Mountains at all scales. Habitat variables are reported for each of the four spatial scales considered (circular plots with radii of 500, 1000, 2000 and 3000 m)

permeability and habitat continuity in the western sector, where this habitat of high value for bears links the more fragmented forest patches of the western landscape matrix.

Forest cover provides a high quality habitat where brown bears can shelter and feed (Clevenger et al. 1992; Mattson et al. 2001; Schrag et al. 2008). However, even if the use of forested landscapes in the eastern sector is higher than in the west, it is the eastern subpopulation which exhibits fewer bears and lower fecundity. This result might suggest that: (1) forest cover, which is still sufficiently large for bear requirements in the west, does not represent a limiting factor for both subpopulations; and (2) heterogeneity of landscape composition is also important, yet previous multi-scale models have shown the value of having large areas of forest intermixed with shrubland (Mateo-Sánchez et al. 2014a). Landscape fragmentation is often perceived as negative due to habitat loss and the breaking apart of habitat (Fahrig 2003). However, habitat fragmentation is not always unfavourable for species. Fragmentation is more than just habitat loss because, by creating small and isolated patches, it also changes the properties of the remaining habitat resulting in a more complex habitat landscape (Fahrig 2003), which can have a positive effect on biodiversity (Huffaker 1958). Actually, the higher human presence and more fragmented forest habitat in the west do not seem to have the expected negative effect on this subpopulation. The same amount of a habitat subdivided into several smaller areas may ensure better habitat distribution and heterogeneity in the matrix (e.g. shorter distances between

Table 2 Model-averaged coefficients and relative importance values (RIV) of each explanatory variable included in the best model or set of models (ΔAICc < 2) describing the difference in habitat use between the western and eastern brown bear subpopulations in the Cantabrian Mountains. β = estimate; *SE*, standard error; *CI*, confidence interval. *p*-values were < 0.0001 for all variables at all scales. Values are shown at each of the spatial scales considered in the analyses (i.e. 500, 1000, 2000 and 3000 m)

Spatial scales	Explanatory variables	β	SE	CI	RIV
500 m	Intercept	3.05	0.07	2.90; 3.19	
	Altitude	− 1.35	0.06	− 1.46; − 1.23	1
	Ruggedness	1.68	0.05	1.58; 1.78	1
	% forest	− 0.29	0.05	− 0.39; − 0.19	1
	% shrubland	0.40	0.06	0.29; 0.51	1
Deviance = 38.0%					
1000 m	Intercept	3.28	0.08	3.12; 3.44	
	Altitude	− 1.60	0.07	− 1.74; − 1.45	1
	Ruggedness	1.59	0.05	1.49; 1.69	1
	River length	− 0.37	0.04	− 0.46; − 0.29	1
	% forest	− 0.16	0.06	− 0.27; − 0.06	0.98
	% shrubland	0.61	0.06	0.49; 0.72	1
Deviance = 43.9%					
2000 m	Intercept	3.18	0.08	3.02; 3.33	
	Altitude	− 1.51	0.07	− 1.65; − 1.37	1
	Ruggedness	1.26	0.05	1.17; 1.35	1
	River length	− 0.48	0.04	− 0.56; − 0.39	1
	% shrubland	0.81	0.05	0.71; 0.91	1
Deviance = 44.9%					
3000 m	Intercept	3.88	0.10	3.67; 4.09	
	Altitude	− 1.12	0.09	− 1.29; − 0.94	1
	Ruggedness	1.99	0.07	1.85; 2.14	1
	River length	− 0.78	0.05	− 0.87; − 0.68	1
	Road length	0.66	0.06	0.55; 0.78	1
	Trail length	1.18	0.07	1.04; 1.33	1
	% forest	− 0.45	0.09	− 0.61; − 0.28	1
	% shrubland	0.66	0.08	0.51; 0.82	1
	% rocky areas	− 0.38	0.05	− 0.49; − 0.28	1
Deviance = 58.4%					

patches of the same category) (Fahrig 2003) and limits the effect of local disturbances (Roff 1974a, 1974b; den Boer 1981). For example, the different arrangement of shrub and forest habitats in the western vs. the eastern sectors might have an impact on the ability to access diverse trophic resources. As a final conclusion, we suggest that landscape characteristics alone might not have the expected role in potentially explaining differences between subpopulations. Indeed, even if some habitat patches offer additional shelter and food to the western subpopulation, characterised by a higher bear density and fecundity, western bears also use less forested areas (a well-known brown bear high-quality habitat for both food and cover) as well as areas with a higher presence of human infrastructures.

Fifteen years ago, the Naves et al. (2003) analysis of the Cantabrian subpopulations drew a not-too-optimistic picture of the condition of brown bear habitat in northern Spain. Indeed, the authors asserted that (a) the two subpopulations occupied a high proportion of suboptimal habitats, and (b) over the long term, the Cantabrian Mountains could be a demographic sink due to the combination of high human impact and low natural habitat quality. However, both the current positive trend of the Cantabrian population and our results seem to show that the dynamics affecting the Cantabrian brown bear subpopulations might be more complex than previously believed and cannot be understood on the basis of habitat analyses only. Indeed, numbers of bears and, particularly, FCOY have increased in both subpopulations since the

Table 3 Characterisation of the habitat structure of the western vs. eastern brown bear subpopulations in the Cantabrian Mountains. For both forest and shrubland cover, we took into consideration: edge density (m/ha, ED), number of patches (NP), largest patch index (%, LPI), mean patch size (ha, MPS) and mean nearest-neighbour distance (m, MNN). Shannon's (SHDI) and Simpson's (SIDI) indices were calculated for the whole landscape surface occupied by brown bears (see the "Methods" section)

Land cover classes	East vs. west	Landscape fragmentation indices				
		ED	NP	LPI	MPS	MNN
Forest	E	17.8	701	6.6	260.8	315.6
	W	20.3	1374	2.1	151.0	273.3
Shrubland	E	2.3	258	0.1	50.4	1132.1
	W	2.5	356	0.1	60.6	1184.9
		SHDI	SIDI			
Whole landscape	E	1.94	0.78			
	W	1.77	0.74			

beginning of this century, even if at a slower rate in the eastern sector of the Cantabrian Mountains. Moreover, since trend data on both subpopulations have been available (i.e. the last 40 years), the eastern subpopulation has always been shown to be 1/3–1/4 that of the western one (Palomero et al. 2007; FAPAS/FIEP 2017). If the habitat use displayed by the two brown bear subpopulations of the Cantabrian Mountains only offers limited help in explaining the differences in number and fecundity exhibited by the evolution of the two subpopulations, other factors might be acting on them. Given that (a) previous population models have partially failed in forecasting the dynamics and trends of brown bears in the Cantabrian Mountains and (b) patterns of increase and fecundity continue to be different between the west and the east (Gonzalez et al. 2016; Penteriani et al. 2018), we suggest that future analyses should be focused more on how the human environment can achieve coexistence with bears than on the natural landscape (Zarzo-Arias et al. 2018). If habitat alone cannot help explain the different properties of the two Cantabrian bear subpopulations, then suspicions may arise around direct human influences on the different trends exhibited by the two sectors of this endangered bear population. For instance, persistence of poaching and/or bad practices during wild boar *Sus scrofa* hunting might be more pronounced in the eastern sector of the Cantabrian Mountains, engendering a higher mortality of more vulnerable bear classes, such as cubs and subadults.

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