Universidade de Évora - Escola de Ciências e Tecnologia

Mestrado em Biologia da Conservação

Dissertação

Brown bear behaviour in human-modified landscapes: the case of the endangered Cantabrian population, NW Spain

Pedro Miguel Matos Cabral

Orientador(es) | Vincenzo Penteriani Dragone
João Eduardo Rabaça

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Resumo

As populações de grandes carnívoros estão a recuperar por toda a Europa após séculos de declínio populacional. A população Cantábrica de urso pardo *Ursus arctos* encontra-se em perigo e é um bom exemplo de um grande carnívoro que habita uma paisagem modificada pelo Homem. A fim de estudar o impacto dos elementos da paisagem humanizada no comportamento do urso pardo, analisamos 10 anos de registos de comportamento de urso pardo Cantábrico. A atividade e estruturas humanas não parecem ter impacto na duração ou no aparecimento do comportamento de vigilância. O urso-pardo evita o contato direto com os seres humanos, no entanto a mera presença de infraestruturas e atividades humanas não parece ter impacto no comportamento de vigilância. O urso-pardo parece estar adaptado à coexistência humana e isso deverá dar uma perspetiva diferente a futuros esforços de conservação.

Palavras-chave: Urso-Pardo; Ursus arctos; Comportamento Animal; Cordilheira Cantábrica; Paisagem

Brown bear behaviour in human-modified landscapes: the case of the endangered Cantabrian population, NW Spain

Abstract

Large carnivore populations are recovering in Europe after centuries of population decline. The Cantabrian brown bear *Ursus arctos* population is endangered, and it is a good example of a large carnivore inhabiting a human-modified landscape. In order to study the impact of human landscape elements on bear behaviour we analysed 10 years of Cantabrian brown bear records. Human activity and structures do not appear to have an impact on the duration or appearance of vigilance behaviour. While bears avoid direct contact with humans, the mere presence of human infrastructure and activities don't not appear to impact its vigilance behaviours. The brown bear seems to be adapted to human coexistence and this should give a different perspective in future conservation efforts.

Keywords: Brown Bear; Ursus arctos; Animal Behaviour; Cantabrian Mountains; Landscape

Introduction

In Europe, Large carnivore populations have been recovering (Chapron et al. 2014) after centuries of population decline (Ripple et al. 2014). This is also the case for brown bear (*Ursus arctos*) populations. (Chapron et al. 2014). Large carnivore recovery is due to favourable changes in legislation (Linnell et al. 2005), changes in public opinion regarding carnivores (Carter & Linnel 2016), and improvement in habitat conditions (Linnell et al. 2005) and since carnivores have a large impact on ecological communities (e.g regulating the number of herbivores; Terborgh et al et al. 2001) their conservation is of major importance (Fernández-Gil et al. 2013). The land that carnivores are returning into is heavily modified by humans (Kuijper et al. 2016). Carnivores diet and large home ranges makes conflicts with humans a recurrent situation (Treves & Karanth 2003) that sometimes turns into consequences such has lethal control and poaching (Fernández-Gil et al. 2013). Studies show that large carnivores have specific sensitivities to human environments (Chapron et al. 2014) and that contact with humans and their activities is a larger threat than stochastic events. Some believe it should be given more attention to solving human related conflicts than combating stochastic events (Woodroffe & Ginsberg, 1998). For apex predators is hard to compensate high mortality rates, especially when inhabiting humanized landscapes (Fernández-Gil et al 2013) The size of nature reserves does not allow for large carnivore population (Linnell et al. 2005, Woodroffe & Gisberg 1998) therefore is necessary to make these species part of the humanized landscape (López-Bao et al. 2017). We need to make plans to minimize the risks of conflict and allow adaptation on both sides (from human and carnivores) to this same coexistence (Carter & Linnell 2016).

Human disturbance can have negative impacts on wildlife. Studies have shown that disturbance can affect reproduction (Antonov & Atanasova 2003; Beale et al. 2004, Estes & Mannan 2003; Giese 1996; Slabbekoorn & Peet 2003), foraging habits and diet composition (Fleischer et al. 2003, Kristan et al. 2004), it can displace animals, impact habitat selection and habitat use (Gander & Ingold 1997; Gill et al. 1997; Markovchick-Nicholls et al. 2007; Prange et al. 2004, Preisler et al 2005; Sutherland & Crockford 1993), change activity patterns and behaviour (Gaynor et al 2018; Jayakody et al 2009; McClennen et al 2001; Riley et al 2003; Tigas et al 2002) and contribute do increased mortality rates (Feare et al. 1976; Forman & Alexander 1998; Wauters et al. 1997).

The disciplines of animal behaviour and wildlife conservations have been working together to better understand conservation problems and guide conservation efforts (Angeloni et al. 2008). Human disturbance has effect on animal behaviour (Tuomainen & Candolin 2010), and since this change in behaviour appear to help the individual cope with the stress caused by human landscapes (Ditchkoff et al. 2006), studying an animal's behaviour is a good way to evaluate the impacts animals suffer for living near human activities (Tuomainen & Candolin 2011).

Brown bears are the ursid with the widest distribution in the world and one of the most widely spread large carnivore. Its conservation status is LC (Least Concern) globaly (McLellan et al 2017) in Spain being considered Endangered (Blanco & Gonzalez 1986). Nevertheless, centuries of persecution eliminated most of the Western European populations (Zedrosser et al. 2011). This case was made worse by loss and fragmentation of the habitat and the specie large spatial requirements (Swenson et al. 2000). In the 20th century a shift to more conservation-oriented management (Zedrosser et al. 2011) allowed the species to recover (Chapron et al. 2014). Some of the main international agreements to protect the species are: The Habitats Directive that includes brown bears has a priority species in the Annex II referring to «Animal and Plant species of community interest whose conservation requires the designation of special areas of conservation». Estonia, Finland and Swedish populations aren't included. Is also included of the Annex IV of the same Directive which includes «Animal and plant species of community interest in need of strict protection» (DL nº 49/2005 of 24 of February). All members of the Ursidae family are part of the Appendix II of the Berna Convention, for strictly protected fauna species (DL nº 316/89 of 22 of September) and is also part of the Annex I and II of the Cites convention (DL nº 50/80 of 23 of July). The European Union also has directives in place in order to protect brown bears (Swenson et al. 2000). The spanish brown bear population is divided in two, the Cantabrian population and the Pyrenees population (FAPAS 2017). In Spain, brown bears are protected since 1973 and the government has developed several recovery plans in the last decades (Perez et al. 2014). Bear incidents are generally related to damage done to apiaries, with some complaints about damage to livestock and agriculture (Bautista et al. 2016).

The Cantabrian population is divided into two sub-populations: The Western and the Eastern, with the western population estimated to have 200 individuals and the Eastern population between 35 and 30 (Fapas 2017). Both populations are genetically differentiated, but recent studies have shown that there is an improving connectivity and gene flow between both (Perez et al. 2010). While their range has areas of low human density, it's also composed of some areas with extensive agricultural and urban development (Mateo-Sánchez 2015).

Brown bears are known for being sensitive to human disturbance (Ordiz et al. 2011) and for adapting their behaviour in order to avoid proximity to humans (Martin et al. 2010). Bears changing their activity patterns and habitat selection (Moe et al. 2007) and avoiding roads (Skuban et al. 2017b), are good examples of human avoidance behaviours. Another source of disturbance is the increasingly popular brown bear viewing activity, where people will gather in locals where they can see brown bears. This can have strong implications specially when occurs in sensitive places where bears appear in groups to feed, mate, or when rearing cubs (Penteriani et al. 2017).

In order to understand if brown bear behaviour was influenced by the human modified landscape, we analysed 10 years of video recordings of brown bears. The first step was analysing the time bears spend on different behaviours in relation to the presence of human landscape features. We then analysed if the presence of human infrastructures influenced the appearance or the duration of the vigilance behaviour, and what impact that change in behaviour had on brown bears. We also accounted for the influence of internal (e.g. age) and external (e.g. natural habitat characteristics and season) factors since and individual behaviours is the complex interactions of both factors.

We hypothesised that if human disturbance has a negative effect on brown bears, that should change their behaviour and bears would increase the time spent in vigilance especially when near humans and their activities. However, if bears have adapted to the coexistence with humans in modified landscapes, no changes in their behaviour should be found as a function of the distance to human environments.

Methods

Study Area

The recording of brown bear behaviour videos was in the western sector of the Cantabrian Mountains, in Spain (Fig.1.), which includes the west of Asturias and north of Léon Autonomous Province. The Cantabrian Mountain Range has an East-West orientation and its maximum altitude is of 2648m. The elevation and average gradient of the north facing slopes are 700 m and 34% respectively, and for the south facing slopes the values are 1300 m altitude and 21% inclination. Due to the proximity to the Atlantic Ocean as well as the orientation of the mountain range, there is abundant rainfall on the north facing slopes, occurring the opposite phenomenon on the south facing slopes due to the barrier effect of the mountains (Naves 2003). The average total precipitation is 900-1900 mm (Martinez Cano et al. 2016). The forest cover differs between both orientations of the slopes, being more varied in the northern slopes composed by oaks (*Quercus petraea*, *Q. pyrenaica* and *Q. rotundifolia*), beech (*Fagus sylvatica*), and chestnut trees (*Castanea sativa*), and in the Southern slopes is mostly composed of oaks (*Q. petraea, Q. pyrenaica*) and Beech. At altitudes between 1700 and 2300 m due to climate, there is no forest growth and scrub (*Juniperus communis*, *Vaccinium uliginosum*, *V. myrtillus*, *Arctostaphylos uva-ursi*) dominates the landscape. Human densities are between 12.1 and 6.1 inhabitants / km^2 in areas that coincide with the Cantabrian brown bear populations (Naves 2003). Human activities resulted in an altered landscape were natural forest gave place to pastures and heathland. However, with the abandonment of rural areas (depopulation rate of ~10% a decade) resulted in recovery of natural habitats (Martinez Cano 2016). The main local economic activities are livestock, mainly cattle raising, tourism, mountain sports, hunting, agriculture and logging and mining (Naves et al. 2003)

Behaviour Analyses

To record Behavioural videos, we used the digiscoping technique (a digital camera and a telescope) that allows to film at a long distance (hundreds of meters, sometimes over 1 km) to not influence bear behaviours. These records were made between 2008 and 2017. In order to classify the behaviours identified in the videos we created an ethogram. Bear behaviours were selected based on ethograms created in other studies (Perdue, 2016) (see table 1.)

Table 1. Ethogram used to analyse brown bear behaviours in the Cantabrian Mountains.

Behaviour	**Description**
Feeding	The bear is actively searching for food or foraging.
Walking	The bear is moving in any direction with no apparent purpose, nor performing other behaviours at the same time.
Resting	The bear is in a still position laying down or sitting with its eyes open or closed (sleeping), and not exhibiting any other behaviour.
Vigilance	The bear is actively interested in some part of is environment, sniffing the air, moving the ears.
Marking	The bear is marking, e.g., on trees or shrubs.
Agression	Contact or non-contact interaction with at least one conspecific, which includes chasing, biting, pawing at or slapping another animal with the paw.
Nursing the Cubs	All interactions between a female with its cubs
Mating	Mating behaviour, e.g., male and female interactions during the mating period.
Social Interaction	Any interaction with at least one conspecific, except mating or aggression, e.g., eye contact with another individual, playing (usually between related subadults), observation of another close bear.
Other	Other behaviours not recognizable or not appearing in the list, e.g., grooming, scratching itself, preparing the den.

Our focus was on vigilance behaviour, since it can be taken as the level of human disturbance affecting the individual bear. It was considered vigilance behaviour when the bear was intensively investigating its surroundings using is sense of smell, hearing or is sight or focusing on a specific direction.

In order to measure the duration of each visualized behaviour, following the ethogram created, we used BORIS behavioural analysis software (http://www.boris.unito.it/pages/download.html). The individual bears in the videos were distributed (when identification was possible) into three categories (hereafter, bear classes) related to their age and gender (i.e. adult, subadult, female with cubs). In some cases, it was possible to identify specific individuals based on their morphology, colour or coat patterns (Fagen and Hagen, 1996; Higashide et al., 2012). No recording could be done during the night, nevertheless daytime records are better in representing human disturbance as they increase the likelihood of bears crossing human activity (humans are more active during the day).

We used the bear cycle in the Cantabrian region (Martinéz Cano et al, 2016) to classify videos according to the season they were recorded. The seasons are: “winter” (from January to mid-April), when most bears hibernate, “spring - early summer” (mid-April to June) bear’s breeding season, and “late summer and autumn” (July to December) the hyperphagia season where food consumption increases in order to accumulate fat reserves for next winter. In the Cantabrian mountain range, not all bears hibernate and when they do so is for a short period (Nores et al, 2010) which allowed records in the winter period (n = 90).

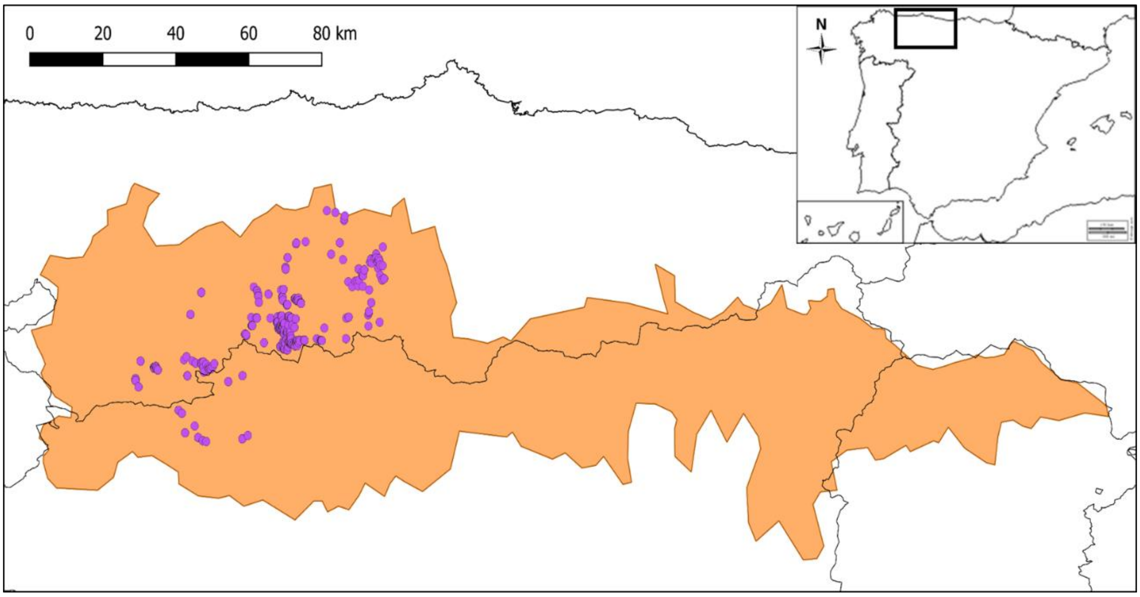

Fig. 1. The locations of the 3 132 videos (78.5 hours in total) of different brown bear behaviours associated with 167 adults, 42 subadults and 112 females with cubs, within the species distribution (orange shape) in the Cantabrian Mountains, Spain.

Environmental variables

Each video had assigned the coordinates of the location where the observation was made. During each observation the bears did not travel long distances, thus allowing the position of each bear to serve has the location of the video. This information made it possible to use the QGIS 3.0.2 program (Team QGD, 2015) in order to analyse the landscape characteristics where each video was recorded and to associate them with the recorded behaviours.

In each video the level of disturbance caused by activities and human presence in the area was measured. This was done by measuring the minimum distance from each record to: (1) paved roads; (2) unpaved roads and trails; and (3) urban settlements. The minimum distance to one of the six most commonly used bear viewing points in the Cantabrian Mountains was also calculated. To obtain the information related to roads, we used CNIG's transportation network information (http://centrodedescargas.cnig.es) and for the urban settlements we used the National Topographic Base BTN100.

Habitat characteristics were also taken into consideration and for this purpose, were considered: (1) altitude; the minimum distance to (2) forests; (3) shrubland; (4) natural open areas (grasslands and pastures) and (5) crops.
In order to calculate the minimum distance to these landscape variables, we used the Forest Map of Spain MFE50 (http://www.mapama.gob.es).
However, in the statistical models the minimum distance to crops and altitude was not used, as the former was highly correlated to urban settlements and trails and the altitude correlated with roads (Pearson correlation coefficients> 0.6).

Statistical analyses

We analysed the association between the duration of recorded behaviours (i.e. walking, feeding, nursing and resting) and the environmental variables, season and bear class, in order to study brown bear behaviours in the human-modified landscapes. So that we could compare recorded behaviours during different times between them, the time of each observed behaviour was divided by the duration of each recorded video. Since there is an intrinsic correlation between recorded behaviours, i.e. when a bear is walking is not resting, we constructed four covariance matrices with dyads of walking and feeding, walking and resting, resting and feeding and nursing and feeding. In order to quantify estimates of variance and covariance components between dyads of the behaviour traits considered, we made four separate models (Doncaster & Davey 2007). The explanatory variables were environmental variables, season and bear class and in all models, year and individual identity were included as random factors. To test the significance of covariance the models were compared with and without the covariance set to 0 using log-likelihood ratio test.

Since we intend to study if the appearance and duration of vigilance/alert behaviour is somehow related to human infrastructures, we built two separate generalized linear mixed-effects models (GLMMs). The first model was used to analyse if the appearance of the vigilance behaviour (binomial variable: 0 = no vigilance behaviour showed by the individual; 1 = appearance of vigilant behaviour) was related to presence of humans and their activities. Natural habitat features (forest, open habitat and shrubland), individual characteristics (i.e. bear class) and season were also included, since brown bear behaviour also depends on external and internal factors. We included presence of humans and natural landscape characteristic as covariates, while individual characteristics and variables related with time were included as factors. The second general linear mixed-effect model was built to study whether the times bears spent alert (vigilance behaviour duration being normally distributed) was dependent on the proximity to different human structures (human settlements, roads, trails and bear viewing points). In this model we again included natural habitat features (forest, open habitat and shrubland), individual characteristics (i.e. bear class) and season. In both models, we accounted for the intrinsic annual variability by the inclusion of the year as random factor, and for the fact that vigilance behaviour is more likely to last longer as the time recorded increases by including the duration of the video as an offset. Since the offset is a structural predictor, whose coefficient is assumed to have the value 1, the values of the offset are simply added to the linear predictor of the target (Bates & Sarkar 2006). We used Akaike's Information Criterion in order to select the best models considering the ones with ΔAIC lower than 2 as competitive. In each set of models, the model averaging was applied on the 95% confidence set in order to derive relative importance values (RIV) and parameter coefficients of each variable using the full -model averaging approach (Burnham & Anderson 2004).

In the variance analysis of variance explained above, we also studied whether time individuals spent alert had influence on brown bear behaviour (i.e. walking deeding, nursing and resting). To do so we analysed the covariances matrices described above against time alert behaviour, bear class, and season as explanatory variables.

All the statistical analyses were performed using R 3.41 statically software (R Core team 2013) using the MuMIn package (Barton 2018) with Ime4 package (Bates & Sarkar 2006) and ASReml-R for bivariate models (Butler et al 2019).

Results

In total 3132 videos were analysed, corresponding to 78.5h of observed bear behaviours. The total number of recorded individuals in each bear class was of 167 adult bears, 42 subadults and 112 females with cubs (Table App2).

Non-vigilant behaviour

Of all behaviours analysed the one bears spend more time on was feeding (54% of the total amount of time recorded) (Table App1). Females with cubs and subadults were the bear classes that spent more time feeding when considering all season (Table App2) (time spent feeding peeked for both classes during the spring-early summer; 5.45±7.62 min, range=0-47.5 min for females with cubs, and 4.26±4.36 min, range=0-14.81 min for subadults).

Adult bears stayed further away from human settlements during 'spring-early summer' and 'late summer autumn' than female with cubs and subadult bears (Table App3). During the winter adult bears were the closest class of bears to human settlement (see also Fig. 2). The models that incorporated the

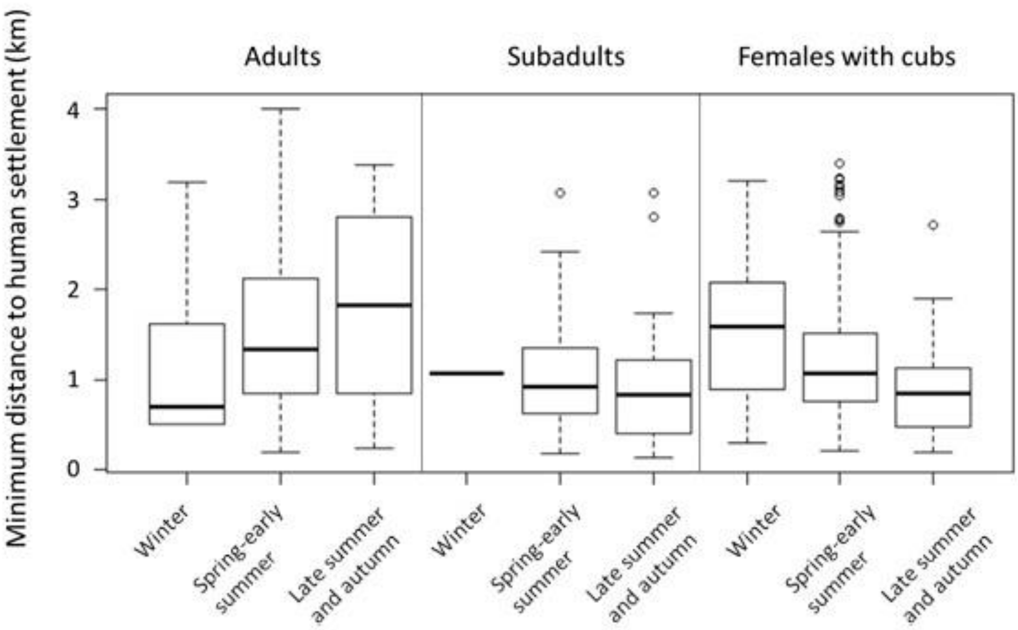

Fig. 2. Distribution of the minimum distance (km) to human settlements (town and villages) of all brown bear observations among the different bear classes (adults, subadults and females with cubs) in each season (winter, spring-early summer and late summer and autum).

covariance of behaviours explained a significant proportion of variance when compared with models that did not included covariance (Table App 4 and 5). We found that there was an association between the dyad feeding and nursing and the human variables (Table App 5). This dyad has a positive covariation associated with viewpoints and a negative covariation associated with human settlements. This result suggest that bears change from feeding to nursing and the other way around more frequently around human settlements, and less frequently around viewpoints.

Appearance and duration of vigilance behaviour

Our results indicate that the appearance of vigilance was related to the duration of the video and with bear class (all RIV=1; Table 2). Adult bears were less likely to exhibit vigilant behaviour than females with cubs and subadults (Fig. 3). There was no strong relation between the appearance of vigilance behaviour and any of the human or natural habitat variables (although their RIV values were above 0.56) (Table 3).

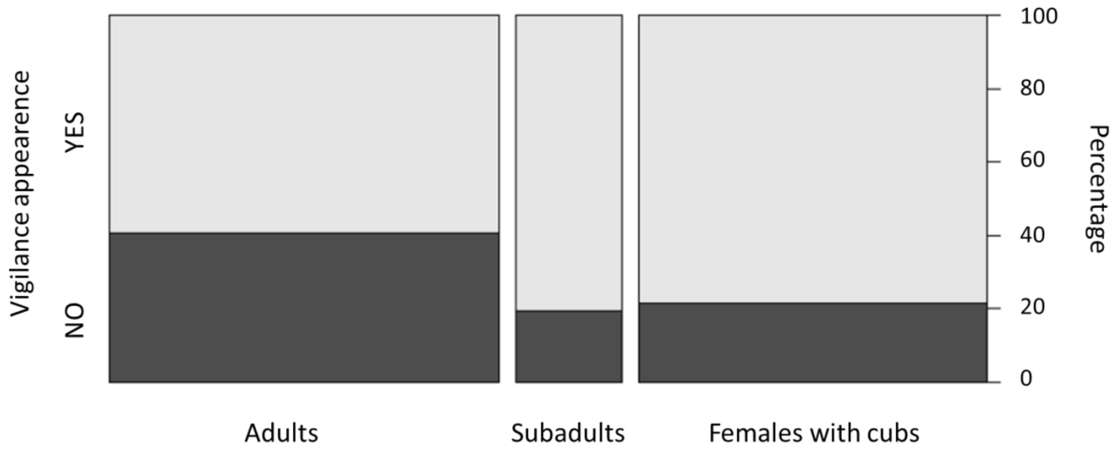

Fig. 3. Distribution of vigilance behaviour appearance among the different bear classes, (adults, subadults and females with cubs.)

The duration of vigilance was related with the duration of the video and with season (Table 4). Bears spend less time in vigilance during the hyperphagia season (i.e Late summer and autumn) than in other seasons (Fig 4). Adult bears spend more time in vigilance during the winter compared with the other bear classes (Fig. 5). Females with cubs spend more time on vigilnace during the mating season (i.e Spring-ealry summer). Of all the combinatios of behaviour, results show that alert duration was negatively associated with the covariance of more than one of the dyads of behaviour (Table App4). Our results indicate there

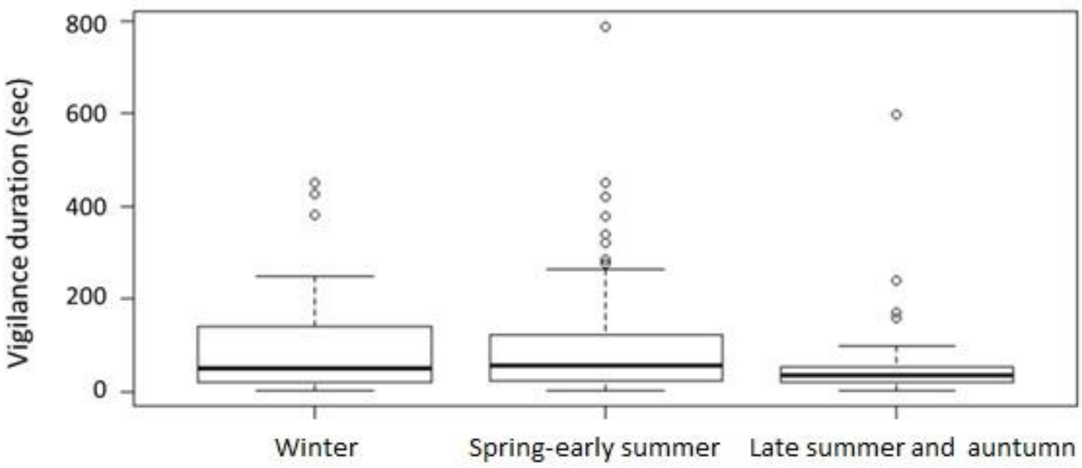

Fig. 4. Distribution of vigilance behaviour duration (in sec) among the different seasons (winter, spring-early summer and late summer and autumn)

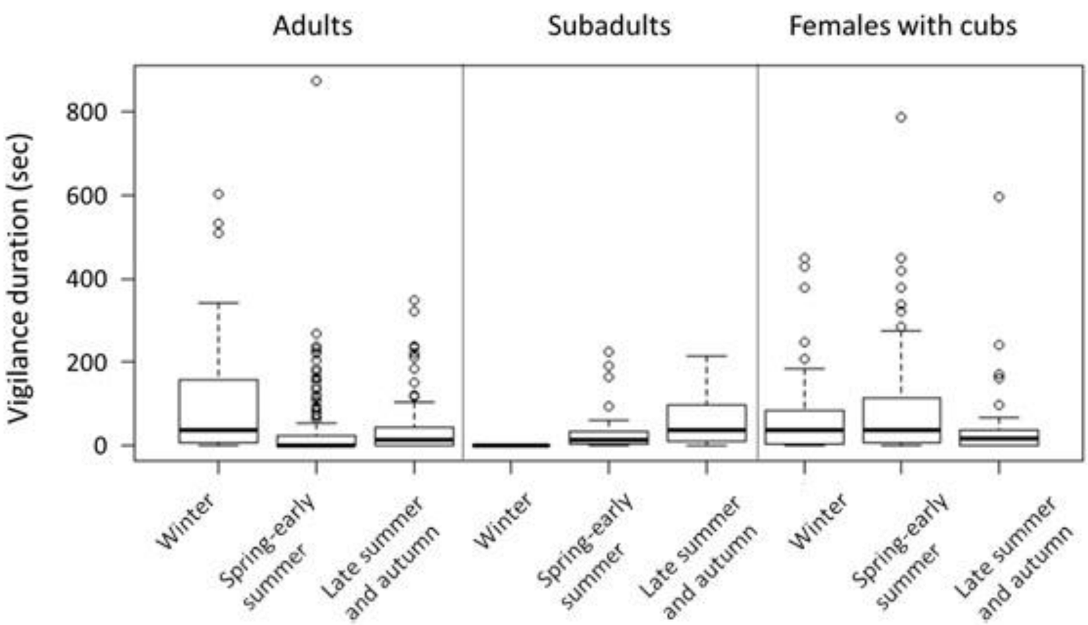

Fig. 5. Distribution of vigilance behaviour duration (in sec) among the different bear classes (adults, subadults, and females with cubs) in each season (winter, spring-early summer and late summer and autum).

is a negative association between alert duration and the covariance of feeding-resting, feeding walking and feeding and nursing (Table App4) Has bears spent more time in vigilance behaviour they choose one of those behaviours or the other. With less time spent on vigilance bears were more likely to display both.

Discussion

The results seem to indicate that the appearance and the duration of the vigilance behaviour are not associated with the presence or proximity to human activities and their structures. This may be because brown bear populations in Europe have high levels of tolerance to human disturbances and to living in humanized environments (Linnell et al. 2005). Bears avoid contact with humans (Ordiz et al. 2013, Moen et al. 2018), even when approaching human settlements (Jerina et al. 2010) and can adapt their behaviour to seasonal, or even daily, changes in human activities. Studies have shown that bears choose beds with greater coverage during the daytime than during the night, in locations closest to human settlements and in periods of increased human activity (e.g. summer / fall and hunting season) (Ordiz et al. 2011). The use of the cover as an avoidance strategy has been studied in European rabbits (*Oryctolagus cuniculus*) that hide in vegetated patches during the day (Moreno et al. 1996) and in females of European Roe Deer (*Capreolus capreolus*) that hide their cubs in denser vegetation (Bongi et al. 2008). This behaviour is especially effective against predators that rely on vision to hunt. Because vision is sense most commonly used by humans for detection, bear searching for cover might indicate an adaptation to the situation of coexistence with people, and to avoid human disturbance (Ordiz et al. 2011).

In Europe, bears tend to be more nocturnal (Kaczensky et al. 2006; Moe et al. 2007; Ordiz et al. 2014) than in other areas of the world (Zedrosser et al. 2011). This change in the pattern of activities happens in order to avoid human encounters (Ordiz et al. 2011). Bears react to a direct encounter with humans by fleeing, as tested by experimentally approached bears (Moen et al. 2018). In Scandinavia, longer periods of nocturnal activity were recorded during the hunting season (Ordiz et al. 2012) and on the days after encounter with humans (Ordiz et al. 2013). The mere presence of human settlements does not appear to change bear activity patterns, however, structures such as roads that are easily associated with human activities seem to have the opposite effect. (Ordiz et al. 2014). All these bear avoidance behaviours are similar to those presented in a predator-prey relationship (Ordiz et al. 2011). Frid & Dil (2001) believe that disturbance stimuli are equivalent to predation risk. Faced with a source of disturbance, animals react by changing their behaviour (e.g., running away, hiding, selecting different habitats or feeding site) at a cost of fitness enhancing activities (e.g. feeding, mating) in the same way they would in the presence of a predator. The fact that some individuals react differently may be because risky behaviours usually translate into potential fitness benefits (Lima & Dill 1990, Lima 1998) along with different individual factors such as previous experience, habituation or physical condition (Tablado & Jenni 2015). Bears faced with human activities tend to adapt their foraging strategy to either: (a) avoid human if they can access resources at different times or locations; or (b) forage in the presence of humans when there is high quality/availability of food (Rode et al. 2006). These behavioural adaptations seem to show once again that bears are adapted to the humanized environment.

Although there was no relationship between vigilance behaviour and human settlements, season still seemed to influence bear behaviour. The mating season is when the cubs-of-the-year are most at risk of infanticide from adult males which may justify the longer period spent at vigilance by females with offspring during spring-early summer (mating season). During hyperphagia (i.e. late summer and autumn) when males no longer pose a threat to the cubs (Bellemain et al. 2006), and bears invest most of their time on feeding (Naves et al. 2006), vigilance levels are low. With human presence being avoided by many of the top predators, some of their prey use areas near human activity as a refuge (Muhly et al. 2011). The use of proximity to human landscapes as a defence against predators (i.e. human shields) has also been detected in moose (*Moose moose*), which have their calves near roads (Berger 2008), and in Mountain Nyala (*Tragelaphus buxtoni*), which approach human settlements in order to avoid predation (Atickem et al. 2014). This type of strategy has also been studied at the intraspecific level in brown bears (Steyaert et al. 2016). Male adult bears are the least tolerant group of bears to human proximity (Smith et al. 2009) which may explain why females with cubs tend to be closer to human settlements, using this proximity as a shield (Elfström et al. 2014b). Females with cubs tend to avoid the same sites used by adult males (Wielgus & Bunnel 1994, Steyaert et al. 2013) and the possibility of infanticide seems to be the main reason (Wielgus & Bunnel 1995, Steyaert et al.

2016). Sub-adult bears also tend to be closer to human settlements (Nelleman et al. 2007) to avoid adult bears that often exhibit aggressive and dominance behaviours (Mueller et al. 2004) and our data confirms that these bear classes are closer to settlements than adult bears (Fig. 2). Since avoiding the hazards associated with conspecifics is the main reason associated with the proximity of certain bear classes to settlements (Elfström et al. 2014b), it is theorized that younger bears and female with cubs consider adult bears a greater danger than humans (Kaczensky et al. 2006, Elfström et al. 2014b). Nursing behaviour being all the interactions between the mother and the cubs (including looking for them), the fact that bears change from feeding to nursing and the other way around when they are closer to human settlements shows that there might be a greater concern for the safety of the young in these places.

DEPENDENT VARIABLE	EXPLANATORY VARIABLE	MODEL-AVERAGED COEFFICIENTS AND RELATIVE IMPORTANCE VALUES			
		β	SE	P	RIV
Vigilance appearance	Intercept	0.716961	0.3137528	0.02249	-
	Duration (offset)	-	-	-	1
	BearClass1: Subadults	1.0642677	0.3514813	**0.00251**	**1**
	BearClass2: Females with cubs	0.8900139	0.2232919	**6.94E-05**	**1**
	Forest	0.2460338	0.1496288	0.1005	0.87
	Open habitat	0.205616	0.1381372	0.13702	0.83
	Human settlement	-0.122839	0.1344691	0.36138	0.62
	Shrubland	0.1004674	0.1258915	0.42524	0.56
	Season1: Mating	-0.2443475	0.3334388	0.46405	0.49
	Season2: Hyperphagia	-0.0715122	0.2623352	0.78554	0.49
	Trail	0.0393377	0.0895955	0.66098	0.36
	Road	0.0093458	0.0635365	0.88325	0.29
	View point	-0.0001425	0.0611096	0.99814	0.28

Table 2. Model averaged coefficients and relative importance values (RIV) for vigilance appearance in relation to the human environment, habitat composition and intrinsic bear characteristics. Vigilance appearance is a binary variable indicating whether there is any vigilance behaviour recorded (1) or not (0). P value and RIV of the variables with a significant effect ($p < 0.05$) are highlighted in bold.

Table 3. Comparison of the competing models built to explain the (a) appearance and (b) duration of brown bear vigilance behaviour in relation to the human environment variables, habitat composition and intrinsic bear characteristics. Vigilance appearance is a binary variable indicating whether there is any vigilance behaviour recorded (1) or not (0) and vigilance duration is a variable which represents the time in seconds each bear spent performing any vigilance behaviour.

DEPENDENT VARIABLE	COMPETING MODELS	df	AIC	ΔAIC	Weight	R^2
Vigilance appearance	BearClass + Forest + OpenHabitat + Shrubland + Duration	7	681.75	0	0.05	0.1292167
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Duration	9	682.13	0.38	0.04	0.1349776
	BearClass + Forest + OpenHabitat + HumanSettlement + Shrubland + Duration	8	682.15	0.41	0.04	0.1352757
	BearClass + Season + Forest + OpenHabitat + Shrubland + Duration	9	682.33	0.59	0.03	0.1338969
	BearClass + Forest + OpenHabitat + HumanSettlement + Shrubland + Trail + Duration	9	682.38	0.64	0.03	0.1370742
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Shrubland + Duration	10	682.71	0.96	0.03	0.1395005
	BearClass + Forest + OpenHabitat + HumanSettlement + Duration	7	683	1.25	0.02	0.1272648
	BearClass + Season + Forest + OpenHabitat + Duration	8	683.08	1.33	0.02	0.1258817
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Trail + Duration	10	683.15	1.4	0.02	0.1361518
	BearClass + Forest + OpenHabitat + Shrubland + Trail + Duration	8	683.21	1.47	0.02	0.1287212
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Shrubland + Trail + Duration	11	683.35	1.61	0.02	0.1416621
	Season + Duration	5	5262.13	0	0.06	0.0721443

Vigilance duration	Season + Viewing point + Duration	6	5262.69	0.55	0.04	0.07451133
	Season + HumanSettlement + Duration	6	5263.69	1.56	0.03	0.0732944
	Season + Forest + Duration	6	5263.89	1.76	0.02	0.07280913
	Season + Shrubland + Duration	6	5264.01	1.88	0.02	0.07179663
	Season + OpenHabitat + Duration	6	5264.12	1.99	0.02	0.07237139
	Season + Road + Duration	6	5264.13	1.99	0.02	0.07232507

Table 4. Model averaged coefficients and relative importance values (RIV) for vigilance duration in relation to the human environment, habitat composition and intrinsic bear characteristics. Vigilance duration is a variable that represents the time in seconds each bear spent performing any vigilance behaviour.

DEPENDENT VARIABLE	EXPLANATORY VARIABLE	MODEL-AVERAGED COEFFICIENTS AND RELATIVE IMPORTANCE VALUES			
		B	SE	P	RIV
Vigilance duration	Intercept	115.66585	16.15628	< 2e-16	
	Season1: Mating	-42.45055	16.51049	**0.01031**	**0.97**
	Season2: Hyperphagia	-57.19988	19.63053	**0.00364**	**0.97**
	Duration (offset)	-	-	-	**0.90**
	Viewing point	2.85842	4.91055	0.56110	0.43
	Human settlement	-1.06782	3.55456	0.76437	0.30
	Forest	0.94335	3.21050	0.76939	0.30
	Shrubland	0.64219	3.24819	0.84366	0.28
	Open habitat	0.56046	2.99271	0.85182	0.28
	Road	0.55080	2.99957	0.85467	0.28
	Trail	-0.08571	2.92292	0.97667	0.26
	BearClass1: Subadults	-1.82044	8.05437	0.82154	0.16
	BearClass2: Females with cubs	0.83250	5.00716	0.86827	0.16

The availability of food of anthropogenic origin is a factor often cited as a reason for proximity to human landscapes (Skuban et al. 2016, Skuban et al. 2017a), however several authors (Mattson 1990, Mueller et al. 2009, Elfström et al. 2014a, Elfström et al. 2014b) believe that is a proximate mechanism, and that the ultimate mechanism is to avoid conspecifics and food sources that may be dominated by them. The proximity of the adult bears class to human's settlements during the winter period may be the safety of this areas for denning during hibernation (Naves & Palomero 2006). Nevertheless, human disturbance may cause bears to abandon their den during winter, especially early in the denning season. Abandoning the den can lead to increased cub mortality, so avoiding disturbances can explain why females with cubs were further away from human settlements in the winter, when compared to other bear classes (Linnell et al. 2000). Since brown bear is an optional hibernator, in those areas where food is available during the winter, the need for dormancy decreases. This may increase the likelihood of finding bears looking for anthropogenic food in this season (Krofel et al. 2017). Since adult bears try to avoid human proximity the most, their higher vigilance levels when they are closer to human settlements may reflect their awareness.

Although levels of vigilance do not vary widely, behavioural variations between individuals can also be attributed to different types of personalities and how they respond to a given situation (Réale et al. 2014). However, when analysing the levels of disturbance, it should be considered that in stressful situations there may be physiological changes that cannot be visually detected by observing individual's behaviours (Herrero et al. 2005; Støen et al. 2015).

Our results revealed that bears may also feed and nurse near touristic viewpoints where people aggregate to spot bears (Table.App 5). Although ecotourism can play an important role in raising conservation awareness, poorly planned ecotourism can have negative impacts in bears because of the close proximity of humans and bears. This can lead to bear displacement, increased vigilance and altered behaviours and activity patterns, human habituation, health and reproductive problems, and even ecological consequences, since bears are a key part of the ecosystem (Penteriani et al. 2017). This calls for a better planning and management and for better conservation measures that protect the specie form this impacts.

Finally, the goodness of fit (R^2) in our results was low. This might be due because of underfitting, i.e. the models were missing other important variables that we did not take into account in our analyses. We could not measure all the external factors acting on the recorded individual, as well as the information's about what that specific bear experienced before the recording. Actually, factors like the health state of the individual or its individual personality (shy *vs*. bold) are extremely difficult to measure.

Conclusions

After centuries of coexistence with human populations, Brown Bears in the Cantabrian range adapted their behaviour to human pressure. The ability to adapt to human disturbance might be key for large carnivore populations that have large home ranges to survive in landscapes dominated and modified by humans. Nevertheless, humans also need to adapt their behaviours if they want to live in proximity with wild species. Behaviour and its variations should be a key aspect when developing new conservations measures and must be taken in account when measuring a species capability to survive in human-modified landscapes. Future studies should try to measure levels of stress by using physiological indicators that can be present and not affect behaviour like heart rate and heart rate variation.

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Appendix

Table App1

Total time dedicated and percentage of each behaviour by each bear class (adults, subadults and females with cubs) in each season to the different behaviours included in the ethogram.

Age	Adults						Subadults				Females with cubs					
Season	Hibernation		Mating		Hyperphagia		Mating		Hyperphagia		Hibernation		Mating		Hyperphagia	
Behaviour	Seconds	%	Seconds	%	Seconds	%	Seconds	%	Seconds	%	Seconds	%	Seconds	%	Seconds	%
Duration	17 545	-	58 571	-	27 761	-	12 356	-	12 939	-	11 956	-	93 918	-	22 016	-
Vigilance	4 334	25	5 376	9	3 927	14	1 263	10	2 101	16	1 905	16	15 581	17	3 714	17
Feeding	5 879	34	23 174	40	14 442	52	9 984	81	8 972	69	8 392	70	54 216	58	13 833	63
Walking	893	5	3 385	6	5062	18	569	5	955	7	997	8	3 511	4	1 133	5
Resting	2 807	16	2 147	4	733	3	439	4	301	2	102	1	6 326	7	2 700	12
Marking	72	0	480	1	114	0	57	0	0	0	332	3	1 085	1	40	0
Aggression	0	0	452	1	0	0	0	0	49	0	0	0	219	0	0	0
Nursing	0	0	61	0	197	1	0	0	14	0	134	1	9 065	10	433	2
Mating	690	4	22 974	39	0	0	0	0	0	0	0	0	3 429	4	24	0
Social interaction	281	2	36	0	3 246	12	39	0	521	4	89	1	35	0	105	0
Other	2 591	15	487	1	40	0	5	0	26	0	6	0	451	0	33	0

Table App2

Mean, standard deviation (SD), minimum (Min) and maximum (Max) duration (in sec) of all the brown bear behaviours during the three seasons ((‘winter’, ‘spring-early summer’ and ‘late summer and autumn’) of the bear cycle (see text for more details) for adults (A), subadults (B) and females with cubs (C).

A Age	Adults					
Season	Hibernation		Mating		Hyperphagia	
Cases	39		160		90	
Nº individuals	16		118		54	
	Mean ± SD	Min - Max	Mean ± SD	Min - Max	Mean ± SD	Min - Max
Duration	450 ± 399	54 - 1 737	366 ± 391	3 - 2 162	308 ± 326	18 - 1 594
Vigilance	111 ± 158	0 - 605	34 ± 87	0 - 876	44 ± 71	0 - 348
Feeding	151 ± 241	0 - 961	145 ± 268	0 - 2 149	160 ± 261	0 - 1 322
Walking	23 ± 77	0 - 457	21 ± 49	0 - 243	56 ± 110	0 - 778
Resting	72 ± 116	0 - 605	13 ± 48	0 - 383	8 ± 25	0 - 186
Marking	2 ± 8	0 - 49	3 ± 22	0 - 257	1 ± 7	0 - 49
Aggression	0 ± 0	0 - 0	3 ± 21	0 - 177	0 ± 0	0 - 0
Nursing	0 ± 0	0 - 0	0 ± 3	0 - 33	2 ± 19	0 - 177
Mating	18 ± 77	0 - 345	144 ± 301	0 - 1 769	0 ± 0	0 - 0
Social interaction	7 ± 37	0 - 226	0 ± 2	0 - 15	36 ± 136	0 - 884
Other	66 ± 116	0 - 364	3 ± 21	0 - 190	0 ± 3	0 - 19

B	Age	Subadults				
Season		Hibernation	Mating		Hyperphagia	
Cases		1	39		38	
Nº individuals		1	23		27	
		Mean[a]	Mean ± SD	Min - Max	Mean ± SD	Min - Max
Duration		130	317 ± 291	18 - 1 123	340 ± 272	18 - 1 068
Vigilance		0	32 ± 52	0 - 225	55 ± 54	0 - 213
Feeding		130	256 ± 262	0 - 889	236 ± 247	0 - 990
Walking		0	15 ± 47	0 - 267	25 ± 56	0 - 315
Resting		0	11 ± 33	0 - 141	8 ± 45	0 - 277
Marking		0	1 ± 7	0 - 40	0 ± 0	0 - 0
Aggression		0	0 ± 0	0 - 0	1 ± 8	0 - 49
Nursing		0	0 ± 0	0 - 0	0 ± 2	0 - 14
Mating		0	0 ± 0	0 - 0	0 ± 0	0 - 0
Social interaction		0	1 ± 4	0 - 22	14 ± 45	0 - 235
Other		0	0 ± 1	0 - 5	1 ± 3	0 - 18

[a] There is only one observation for subadults in this period.

C	Age	Females with cubs					
Season		Hibernation		Mating		Hyperphagia	
Cases		50		166		43	
Nº individuals		23		74		30	
		Mean ± SD	Min - Max	Mean ± SD	Min - Max	Mean ± SD	Min - Max
Duration		440 ± 432	8 - 2134	566 ± 740	16 - 6 063	278 ± 304	1 - 1 503
Vigilance		74 ± 107	0 - 450	94 ± 185	0 - 1 707	44 ± 100	0 - 597
Feeding		277 ± 342	0 - 1 386	327 ± 457	0 - 2 850	195 ± 240	0 - 854
Walking		23 ± 47	0 - 261	21 ± 55	0 - 534	23 ± 49	0 - 190
Resting		54 ± 127	0 - 575	38 ± 165	0 - 1 744	2 ± 12	0 - 79
Marking		1 ± 6	0 - 40	7 ± 68	0 - 854	8 ± 21	0 - 91
Aggression		0 ± 0	0 - 0	1 ± 17	0 - 219	0 ± 0	0 - 0
Nursing		9 ± 26	0 - 163	55 ± 140	0 - 919	3 ± 11	0 - 45
Mating		0 ± 3	0 - 24	21 ± 158	0 - 1 769	0 ± 0	0 - 0
Social interaction		2 ± 15	0 - 105	0 ± 2	0 - 21	2 ± 10	0 - 59
Other		1 ± 5	0 - 33	3 ± 16	0 - 172	0 ± 1	0 - 6

Table app3 - Mean, standard deviation (SD), minimum (min) and maximum (max) distance (in meters) to human structures and habitats during the three seasons ((‘winter’, ‘spring-early summer’ and ‘late summer and autumn’) for adults (A), subadults (B) and females with cubs (C).

A Age	Adults																	
Season	Hibernation						Mating						Hyperphagia					
	Mean	±	SD	min	-	max	Mean	±	SD	min	-	max	Mean	±	SD	min	-	max
Trails	230	±	161	4	-	698	335	±	186	15	-	857	572	±	372	0	-	988
Roads	503	±	378	115	-	1 884	658	±	623	92	-	4 085	561	±	434	119	-	2 060
Human settlements	1 074	±	714	502	-	3 181	1 618	±	934	196	-	4 705	1 801	±	1 009	245	-	3 380
Viewing points	5 547	±	3 028	97	-	12 450	4 842	±	4 287	97	-	16 428	2 581	±	3 239	478	-	12 450
Forest	19	±	44	0	-	189	46	±	81	0	-	416	41	±	95	0	-	442
Open habitat	965	±	609	0	-	2 447	915	±	816	0	-	3 195	1 149	±	748	0	-	3 117
Shrubland	438	±	301	0	-	693	152	±	217	0	-	982	159	±	192	0	-	784

B Age	Subadults												
Season	Hibernation	Mating						Hyperphagia					
	Mean[a]	Mean	±	SD	min	-	max	Mean	±	SD	min	-	max
Trails	**273**	224	±	203	5	-	1 068	297	±	293	1	-	999
Roads	**130**	448	±	371	3	-	1 196	614	±	497	25	-	1 932
Human settlements	**1 064**	1 059	±	610	181	-	3 061	1 019	±	779	134	-	3 064
Viewing points	**1 093**	3 667	±	3046	97	-	14 923	2 696	±	2 429	478	-	9 681
Forest	**0**	65	±	75	0	-	213	60	±	87	0	-	403
Open habitat	**1 391**	1 214	±	788	16	-	2 724	1 224	±	996	0	-	3003
Shrubland	**452**	64	±	134	0	-	592	102	±	171	0	-	584

[a] There is only one observation for subadults in this period

C	Age	Females with cubs																	
Season		Hibernation						Mating						Hyperphagia					
		Mean	±	SD	min	-	max	Mean	±	SD	min	-	max	Mean	±	SD	min	-	max
Trails		328	±	193	22	-	948	336	±	180	8	-	886	235	±	179	11	-	712
Roads		418	±	301	70	-	1429	624	±	525	9	-	2230	490	±	462	38	-	1769
Human settlements		1540	±	767	297	-	3204	1252	±	741	206	-	3387	913	±	518	194	-	2715
Viewing points		5735	±	3562	516	-	15820	5840	±	4963	97	-	17285	4991	±	4084	560	-	14774
Forest		33	±	95	0	-	501	63	±	82	0	-	359	49	±	94	0	-	337
Open habitat		606	±	412	0	-	1692	933	±	782	0	-	3367	1059	±	862	0	-	2956
Shrubland		200	±	221	0	-	701	109	±	180	0	-	693	189	±	254	0	-	776

Table App4 - Association between the covariance of different behaviours and duration of stress response for brown bears in the Cantabrian Mountains (see 2. Methods for details on the models).

	Variable	Estimate	df	Wald	P
Feeding-resting	Intercept		2	639.66	<0.001
Sig cov: p=0.001	Stress duration	-0.234 ± 0.023	1	96.99	**<0.001**
	Age		2	8.66	<0.001
	Adult	0			
	Subadult	0.059 ± 0.018			
	Female with cubs	0.053 ± 0.012			
	Season		2	24.01	0.013
	Hibernation	0			
	Mating	-0.049 ± 0.016			
	Hyperphagia	-0.049 ± 0.019			
Resting-walking	Intercept		2	108.203	<0.001
Sig cov: p=0.854	Stress duration	-0.031 ± 0.023	1	1.657	0.198
	Age		2	3.087	0.213
	Adult	0			
	Subadult	-0.023 ± 0.018			
	Female with cubs	-0.020 ± 0.012			
	Season		2	7.842	0.01982
	Hibernation	0			
	Mating	-0.048 ± 0.017			
	Hyperphagia	-0.041 ± 0.019			
Feeding-walking	Intercept		1	721.01	<0.001
Sig cov: p=0.002	Stress duration	-0.256 ± 0.025	2	96.35	**<0.001**
	Age		2	15.35	<0.001
	Adult	0			
	Subadult	0.060 ± 0.022			
	Female with cubs	0.052 ± 0.015			
	Season		2	6.72	0.034
	Hibernation				
	Mating	-0.005 ± 0.019			
	Hyperphagia	0.031 ± 0.022			
Nursing-feeding	Intercept		1	676.30	<0.001
Sig cov: p=0.060	Stress duration	-0.110 ± 0.017	2	40.13	**<0.001**
	Age		2	75.47	<0.001
	Adult	0			
	Subadult	0.031 ± 0.013			
	Female with cubs	0.074 ± 0.008			
	Season		2	5.15	0.075
	Hibernation				
	Mating	0.024 ± 0.011			
	Hyperphagia	0.012 ± 0.013			

Table App5 - Association between the covariance of different behaviours and environmental variables for brown bears in the Cantabrian Mountains (see 2. Methods for details on the models).

Dependent variable	Explanatory term	Estimate	Df	Wald statistic	Pr(Chisq)
Feeding-resting					
Sig cov: p=0.003	Estimate		2	647.52	<0.001
	Trail	0.000002377973 ± 0.00002817721	1	1.03	0.309
	Road	-0.00001422876 ± 0.00001319897	1	3.47	0.062
	Population	-0.000006698541 ± 0.000009335185	1	1.05	0.305
	Viewpoint	-0.0000008867574 ± 0.000001589525	1	0.02	0.898
	Forest	0.00004822027 ± 0.00007104066	1	0.81	0.366
	Open area	0.000001439187 ± 0.000007901669	1	0	0.957
	Shrub	-0.00001260678 ± 0.00003067264	1	0.08	0.779
	Age		2	10.48	**0.005**
	Adult	0			
	Subadult	0.03483288 ± 0.0200567	1.7367208		
	Female with cubs	0.03773566 ± 0.01353378	2.7882576		
	Season		2	8.83	**0.012**
	Hibernation	0			
	Mating	-0.05123261 ± 0.01831624			
	Hyperphagia	-0.05871958 ± 0.02108495			
Feeding-walking					
Sig cov: p=0.006	Estimate		2	630.69	<0.001
	Trail	0.000007639117 ± 0.00003364863	1	0.04	0.842
	Road	-0.000006213665 ± 0.00001573358	1	0.01	0.941
	Population	0.00001358491 ± 0.0000112485	1	0.06	0.800
	Viewpoint	-0.000000422118 ± 0.000001928767	1	0.97	0.324
	Forest	0.0001156135 ± 0.00008264027	1	2.45	0.117
	Open area	0.00001685135 ± 0.000009398256	1	3.3	0.069
	Shrub	0.000009025442 ± 0.00003611364	1	0.05	0.817

	Age		2	8.31	**0.016**
	Adult	0			
	Subadult	0.04455599 ± 0.02478221			
	Female with cubs	0.04419866 ± 0.01677296			
	Season		2	3.37	0.186
	Hibernation	0			
	Mating	-0.004757785 ± 0.02132428			
	Hyperphagia	0.02419377 ± 0.024599			
Resting-walking					
Sig cov: p=0.001	Estimate		2	110.43	<0.001
	Trail	0.00001359865 ± 0.00002740033	1	1.536	0.215
	Road	-0.0000252366 ± 0.00001293281	1	2.442	0.118
	Population	0.00001467776 ± 0.000009149365	1	3.083	0.079
	Viewpoint	0.000001051238 ± 0.000001559227	1	0.023	0.879
	Forest	0.00003011914 ± 0.00006923074	1	0.038	0.845
	Open area	0.00001405256 ± 0.000007740065	1	3.15	0.076
	Shrub	-0.000001377284 ± 0.00002992615	1	0.304	0.581
	Age		2	1.771	0.413
	Adult	0			
	Subadult	-0.01969695 ± 0.01970204			
	Female with cubs	-0.01798043 ± 0.01339476			
	Season		2	6.616	**0.037**
	Hibernation	0			
	Mating	-0.04575061 ± 0.01778761			
	Hyperphagia	-0.04034224 ± 0.02031587			
Feeding-nursing					
Sig cov: p<0.001	Estimate		2	639.44	<0.001
	Trail	0.0000214035 ± 0.0000194367	1	0.01	0.922
	Road	0.000008253989 ± 0.000009096992	1	0.37	0.543
	Population	-0.000005231529 ± 0.000006411933	1	5.93	**0.015**
	Viewpoint	0.000001871871 ± 0.000001094458	1	10.05	**0.002**

Forest	-0.000006007738 ± 0.00004929487	1	0.4	0.526
Open area	0.000000125456 ± 0.000005432183	1	0.06	0.809
Shrub	-0.000008901726 ± 0.00002111216	1	2.81	0.094
Age		2	51.84	**<0.001**
Adult	0			
Subadult	0.0187464 ± 0.01376408			
Female with cubs	0.06531672 ± 0.009159461			
Season		2	5.67	0.059
Hibernation	0			
Mating	0.025342 ± 0.01249231			
Hyperphagia	0.01041436 ± 0.01449922			