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# New insights on the behaviour and ecology of brown bears (*Ursus arctos*) in human-modified landscapes. The case of the Cantabrian population

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# Nuevos aspectos del comportamiento y de la ecología del oso pardo (*Ursus arctos*) en ambientes humanizados. El caso de la población cantábrica

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# RESUMEN DEL CONTENIDO DE TESIS DOCTORAL

| **1.- Título de la Tesis** | |
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| Español/Otro Idioma:<br>Nuevos aspectos del comportamiento y de la ecología del oso pardo (*Ursus arctos*) en ambientes humanizados. El caso de la población cantábrica. | Inglés:<br>New insights on the behavior and ecology of brown bears (*Ursus arctos*) in human-modified landscapes. The case of the Cantabrian population. |

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## RESUMEN (en español)

En esta tesis se investigan nuevos aspectos poco estudiados del comportamiento y ecología del oso pardo en ambientes humanizados, tomando como ejemplo la población cantábrica. En entornos como este es crucial entender el comportamiento y la ecología de la especie con el fin de conservar y manejar poblaciones tan únicas. Este es el objetivo general para el que se ha planteado esta tesis, estructurada en cinco capítulos:

**Cap. 1. Hibernación en el oso pardo:** La hibernación es una adaptación para sobrevivir ante condiciones ambientales desfavorables. Se realizó una revisión bibliográfica centrada en tres aspectos: cronología de la hibernación, selección de las oseras y fisiología de la hibernación. Se encontró que la cronología de la hibernación varía entre grupos de sexo y edad, pero también con la latitud. Además, la elección de las oseras parece determinar el estado físico de los individuos y responde a selección de hábitat a gran y pequeña escala. Asimismo, las adaptaciones fisiológicas acaecidas durante la hibernación permiten a los osos sobrevivir a este periodo de privación e inmovilidad. Por último, se diferenciaron los verdaderos desencadenantes de la hibernación de sus correlatos.

**Cap. 2. El papel de las temperaturas primaverales en la fecha de emergencia de las oseras de las osas con crías del año en el suroeste de Europa:** La cronología de la hibernación en los osos pardos obedece a cambios en el ambiente, y presenta cierta flexibilidad de cara a lidiar con sus posibles variaciones. Se investigó los desencadenantes del fin de la hibernación en la única cohorte con hibernación obligada, las hembras gestantes. Se encontró que la fecha de emergencia de las oseras es más temprana conforme aumenta la temperatura máxima en el mes anterior a la emergencia. También se contrastó cómo esta fecha concuerda con el gradiente latitudinal reportado en otras poblaciones. Estos hallazgos son de gran importancia de cara a prever y mitigar los efectos del Cambio Global sobre un periodo tan sensible de la biología de la especie, ya que desajustes en esta cronología pueden tener consecuencias sobre la condición física y la supervivencia de los individuos.

**Cap. 3. Comportamiento de marcaje en el oso pardo europeo. Factores que determinan la selección y densidad de los árboles de marcaje:** El comportamiento de marcaje químico es el más común en muchas especies de mamíferos, incluido el oso pardo, el cual lo desarrolla preferentemente frotándose contra árboles. Se investigó la selección de estos árboles de marcaje, así como los factores que determinan su abundancia. Se encontró que los árboles de marcaje presentan características que los hacen más conspicuos, al ser árboles de mayor tamaño y aislados del resto, lo que se traduce en una mayor facilidad de marcaje y de recepción de la señal química, así como una selección positiva por abedules y coníferas. Por otro lado, la densidad de estos árboles

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no se encontró relacionada con su posición dentro del área osera ni con la abundancia de observaciones de oso en las proximidades.

**Cap. 4. Marcaje visual en mamíferos probado por primera vez mediante manipulación del comportamiento de descortezado en osos:** En la literatura científica se ha infravalorado la capacidad de comunicación visual de algunos grupos animales como los mamíferos, pese a existir razones para pensar lo contrario. Se llevó a cabo un experimento para comprobar si las marcas realizadas por algunos osos en los árboles tienen una función visual, teniendo en cuenta el contraste de color de las marcas y la especie de árbol. Se demostró este comportamiento, realizado por machos en época de apareamiento lo que parece estar relacionado con la reproducción de la especie. Se sugiere que la señalización visual es un mecanismo de comunicación más ampliamente empleado por los mamíferos de lo anteriormente considerado.

**Cap. 5. La influencia de la red de carreteras en la distribución espacial y la idoneidad de hábitat de un gran carnívoro en ambientes humanizados:** Las carreteras son una de las infraestructuras que más impacto tienen en la fauna. En este capítulo se evaluó su potencial impacto en la localización de los osos pardos cantábricos. Se tuvieron en cuenta en cuenta tanto los efectos directos de las carreteras como los efectos indirectos sobre la idoneidad de hábitat. Se encontró que las variables de entorno y poblacionales consideradas tenían un escaso efecto, mientras que la presencia de carreteras apenas modificó la calidad del hábitat. Estos osos, al igual que otras poblaciones con coexistencia histórica con los humanos parecen haber desarrollado cierta tolerancia a la presencia y uso de las carreteras, en contraposición con las poblaciones menos habituadas como las norteamericanas.

## RESUMEN (en Inglés)

This thesis assesses new and little studied aspects of brown bear behavior and ecology in human-modified landscapes, taking the Cantabrian population as an example. In such environments it is crucial to understand the behavior and ecology of the species in order to conserve and manage such unique populations. This is the general objective of this thesis, structured in five chapters:

**Chap. 1. Denning in brown bears:** Hibernation is an adaptation to survive in unfavourable environmental conditions. A literature review was carried out focusing on three aspects: hibernation chronology, selection of winter dens and hibernation physiology. We found that the timing of hibernation varies between sex and age groups, but also with latitude. In addition, the choice of hibernation sites seems to determine the physical condition of individuals and responds to large- and small-scale habitat selection. Likewise, physiological adaptations during hibernation allow bears to survive this period of deprivation and immobility. Finally, the true triggers of hibernation were differentiated from their correlates.

**Chap. 2. The role of spring temperatures in the den exit of female brown bears with cubs in southwestern Europe:** The timing of hibernation in brown bears is driven by changes in the environment, and presents some flexibility in dealing with its possible variations. We investigated the triggers for the end of hibernation in the only cohort with obligate hibernation, the pregnant females. We found that the date of emergence of female bears is earlier as the maximum temperature increases in the month prior to emergence. We also contrasted how this date agrees with the latitudinal gradient reported in other populations. These findings are of great importance in order to foresee and mitigate the effects of global change on such a sensitive period in the biology of the species, since mismatches in this chronology can have consequences on the physical condition and survival of individuals.

**Chap. 3. Rubbing behaviour of European brown bears: factors affecting rub tree selectivity and density:** Chemical marking behaviour is the most common in many mammalian species, including the brown bear, which develops it preferentially by rubbing against trees. The selection of these marking trees was investigated, as well as the factors that determine their abundance. It was found that the marking trees present characteristics that make them more conspicuous, being larger trees and isolated from the rest, as well as a positive selection by birches and conifers, which

translates into greater ease of marking and reception of the chemical signal. On the other hand, the density of these trees was not found to be related to their position within the bear area nor to the abundance of bear observations in the vicinity.

**Chap. 4. Visual marking in mammals first proved by manipulations of brown bear tree debarking:** The visual communication ability of some animal groups such as mammals has been underestimated in the scientific literature, despite reasons to believe otherwise. An experiment was carried out to test whether the marks made by some bears on trees have a visual function, taking into account the colour contrast of the marks and the tree species. This behaviour was demonstrated to be performed by males during mating season, which seems to be related to the reproduction of the species. It is suggested that visual signalling is a communication mechanism more widely employed by mammals than previously considered.

**Chap. 5. The influence of road networks on a large carnivore spatial distribution and habitat suitability in a human-modified landscape:** Roads are one of the infrastructures that have the greatest impact on wildlife. In this chapter, their potential impact on the location of Cantabrian brown bears was evaluated. Both direct effects of roads and indirect effects on habitat suitability were taken into account. It was found that the environmental and population variables considered had little effect, while the presence of roads hardly modified habitat quality. These bears, as well as other populations with historical coexistence with humans, seem to have developed a certain tolerance to the presence and use of roads, as opposed to less habituated populations such as those in North America.

**SR. PRESIDENTE DE LA COMISIÓN ACADÉMICA DEL PROGRAMA DE DOCTORADO EN BIOGEOCIENCIAS**

“*I understood at a very early age that in nature, I felt everything I should feel in church but never did. Walking in the woods, I felt in touch with the universe and with the spirit of the universe.*”

— Alice Walker

“*There is no fundamental difference between man and animals in their ability* to feel pleasure and pain, happiness, and misery.”

— Charles Darwin

*Cuando voy pa la braña nun tsevo pena...*

# Table of contents

# General introduction

The human-modified (or human-dominated or multi-use, hereafter HML) landscape concept is widely represented in the current scientific literature, particularly in the fields of ecology, behaviour and conservation. HML could be defined as environments characterized by the widespread presence of people, human activities, and infrastructures (Morales-González et al. 2020). Human activity has profoundly altered natural habitats (Crutzen 2002), changing the structure and functioning of ecosystems and modifying the biodiversity, biogeochemistry, geomorphology and climate of the planet, where 70% of terrestrial habitats and their processes are significantly altered (Ellis et al. 2013; Newbold et al. 2015). Therefore, the conceptual framework of human-modified environments is being increasingly taken into account when developing conservation and species management actions (Miller and Hobbs 2002; Chazdon et al. 2009). Despite human-induced modification of the natural environment, animal species that inhabit HML have managed to adapt to a greater or lesser extent in response to anthropic pressures, either through changes in behaviour, in their range of distribution or in the timing of their activities (Ciuti et al. 2012; Johann et al. 2020; Srivastava et al. 2021). Indeed, changes in some activities as foraging, movements, resting, vigilance and reproduction have been described, together with their consequences on the physical and on physiological condition of individuals and ecological functions such as population dynamics and species co-occurrence, among others (Ciuti et al. 2012; Wilson et al. 2020).

The increasing human impact on ecosystems has been exacerbated by climate change in these last decades (Wiederholt and Post 2010). Global warming threatens biodiversity by altering habitats, the availability and abundance of resources and microclimatic conditions, in addition to increasing extinction rates (Malhi et al. 2008; Maiorano et al. 2011; IUCN 2014; Pimm et al. 2014). Moreover, climate change modifies the distribution and abundance of wild plants and animals (Root et al. 2003; Parmesan 2006), which is especially important in vulnerable species that are usually geographically restricted, and even more so if they are found in highly anthropized or fragmented environments (Fahrig 2007; Pimm et al. 2014). Faced with fluctuations derived from climate change, species frequently show certain resilience and develop adaptive responses through microevolutionary processes or phenological plasticity (Dawson 2011; Karell et al. 2011; Bellard et al. 2012; Radchuk et al. 2019).

Generally, large mammals are among the species most sensitive to anthropogenic pressure and alterations (Ripple et al. 2014; Faurby and Svenning 2015). Large carnivores are the paradigm of this vulnerability, being at the top of the trophic chains and frequently coming into conflict with humans when competing for feeding resources and threaten people or livestock (Bombieri et al. 2018), which has caused them to be persecuted and extirpated locally (Lamb et al. 2020). Faced with historical persecution and loss of habitat by human activities, large carnivores often exhibit behavioural adaptations allowing to a certain extent their coexistence with humans when they share the same landscapes (Fuller and Sievert 2001; Støen et al. 2015; Carter and Linnell 2016). For example, many large carnivores have shifted to more twilight and/or nocturnal habits in environments with high human presence (Odden et al. 2014; Suraci et al. 2019; Zeller et al. 2019), restricting their activity to more remote areas where human density decreases (Evans et al. 2017; Suraci et al. 2019). However, HML can also attract large carnivores due to the availability of food resources and shelter (Waite et al. 2007; Evans et al. 2017).

In HML, the presence of large carnivores had become increasingly rare in previous centuries having become extinct in many areas or countries due to human action (Ripple et al. 2014; Chapron and López-Bao 2016).. In Europe, large carnivores frequently occupy areas with a high degree of human intervention and density, where these species and humans have adapted in order to coexist (Støen et al. 2015; López-Bao et al. 2017). Even so, in Europe you can still find Eurasian lynxes (*Lynx lynx*), grey wolves (*Canis lupus*) and brown bears (*Ursus arctos*), whose populations are recovering in many areas (Chapron et al. 2014). A common mistake is to consider carnivorous populations only viable in protected or wild areas (López-Bao et al. 2017), without taking into account that their survival or recovery in European HML is resulting from their capacity to adapt to human activities (Zarzo-Arias et al. 2018). However, in the XXI century, the conservation of populations of large carnivores, particularly those that inhabit densely populated areas or highly altered by humans, constitutes one of the paradigms of conservation ecology and biology (Inskip and Zimmermann 2009; Chapron and López-Bao 2016; Lamb et al. 2020). Thus, it is necessary to consider these species as an integral part of anthropized environments (Mace 2014; Carter and Linnell 2016), without which they lose a large part of their geographic range and towards which their future recolonization will mostly develop (Di Minin et al. 2016; Milanesi et al. 2017).

The brown bear population on the European continent is around 17,000 individuals (Penteriani et al. 2020a), although its distribution is restricted to specific areas, occupying mainly wooded and mountainous areas with different uses such as logging, hunting and grazing (Carter and Linnell 2016). In HML, like other large carnivores, brown bears have adapted their behaviour to the presence and human activities (Ordiz et al. 2011, 2012; Penteriani et al. 2020a). In southern Europe, brown bears have coexisted with humans since ancient times, having historically been persecuted almost to their extermination in recent centuries (Zedrosser et al. 2011; Martínez Cano et al. 2016). The small surviving populations are found in mountainous areas, isolated from each other and generally inhabiting areas with significant human presence (Penteriani et al. 2020a). Individuals from these populations have some peculiar characteristics compare to others from more northern populations, such as their markedly vegetarian diet (Bojarska and Selva 2012) and a set of behavioural, physiological, genetic and habitat selection adaptations resulting from isolation and from the continuous and prolonged human presence in their ranges (Colangelo et al. 2012; Benazzo et al. 2017; Zarzo-Arias et al. 2018; de Gabriel Hernando et al. 2020). This is the case of the brown bear population inhabiting the Cantabrian Mountains, in the northwest of the Iberian Peninsula. This population is threatened (BOE 2011) and isolated from other populations for at least 300 km, with a small population of about 300 individuals divided into two nuclei (250 in the west and 50 in the east, (Pérez et al. 2014; López-Bao et al. 2020), and with low exchange and genetic variability (García-Garitagoitia et al. 2007; Gregório et al. 2020). Despite having been reduced to less than one hundred individuals during the 90th, this population has experienced a slow but constant recovery with little or no human intervention (Penteriani et al. 2020a). The Cantabrian brown bear population inhabits a highly anthropized territory with a high human population density, where activities such as cattle ranching and mountain agriculture, human development and transport networks (Mateo-Sánchez et al. 2016; Penteriani et al. 2020b) fragment the optimal habitat and affect the behaviour and ecology of brown bears (Mateo-Sánchez et al. 2016; Zarzo-Arias et al. 2018; Penteriani et al. 2020b). With a small population size and its potential expansion range in areas highly anthropized (Penteriani et al. 2019; Zarzo-Arias et al. 2019), it is crucial to understand brown bear behaviour and its ecology in order to manage and conserve such a unique population. Moreover, Cantabrian brown bears may be more affected by the current global change by living in a mountainous area and marginal climatic areas, such as the Cantabrian Mountains, which are changes in temperature and precipitation patterns associated with current global change (Root et al. 2003; Brunetti et al. 2009). In particular, as a result of these changes, direct loss of habitat and also a decrease in phenological imbalances of trophic resources of bears have been predicted (Penteriani et al. 2019). This may affect their physical condition, increase competition with other species, change movement patterns and force them towards a more carnivorous diet, which can force these individuals to look for foods of anthropic origin such as crops, livestock, hives or garbage, and be the cause of increasing conflict between bears and humans and mortality (Penteriani et al. 2019; Zarzo-Arias et al. 2020).

Brown bears are an "umbrella" for many of the flora and fauna species with which they cohabit, as well as a "flag" species that arouses interest in the conservation of their habitats (Linnell et al. 2000; Zarzo-Arias 2020). Additionally, the brown bears play a double role of vital importance for the ecosystems in which it inhabits, actively participating in biogeochemical cycles (Helfield and Naiman 2006; Rosenblatt et al. 2013), intervening in forest dynamics (Zyśk-Gorczyńska et al. 2015), controlling herbivore populations (Zager and Beecham 2006; Swenson et al. 2007a) and dispersing seeds (Lalleroni et al. 2017; García-Rodríguez et al. 2021). Likewise, like other large carnivores, the conservation of this species allows maintaining ecological functions and recovering ecosystems and their functions (Chapron et al. 2014; Ripple et al. 2014), increases the biodiversity and heterogeneity of ecosystems (Ritchie et al. 2012), regulates food chains (del Rio et al. 2001) and even controls spreading of infectious diseases (Packer et al. 2013; Tanner et al. 2019). Besides, brown bears provide additional economic benefits derived from nature tourism (Penteriani et al. 2017; Richardson 2017).

The general objective of my doctoral thesis has been to cover part of the knowledge gaps as an essential piece for the conservation and management of Cantabrian brown bears. Here, I have prevalently focused my scientific interest on diverse aspects of brown bear biology and behaviour that have the potential to be affected by humans, such as hibernation, intraspecific communication and distribution in relation to the effects of human activities.

I have structured my thesis around five main objectives:

**Chapter I. Denning in brown bears:** The scientific explorations on Cantabrian bears started by firstly addressing one of the key periods in the life cycle of the species, the hibernation, a biological process of some mammals and ursids. In this chapter, the current scientific information on brown bear hibernation was have critically synthesized in a review that covers the three basic aspects of this period: (1) den chronology, (2) den characteristics and surroundings and (3) hibernation physiology and the potential energetic costs.

**Chapter II. The role of spring temperatures in the den exit of female brown bears with cubs in southwestern Europe:** In this chapter, the general approach of the first chapter was shifted to the specific case of brown bear hibernation in the Cantabrian Mountains. By doing this, the role of temperature and precipitation and their interannual variation in the date of den exit of females with cubs were analysed. Females with cubs do not hibernate only in response to food shortage and therefore the factors that trigger den exit in them may be more complex than those that trigger den exit in other sex and age cohorts of brown bears. Current changes in climate might trigger earlier den exit dates, with potential consequences on the population dynamics of brown bears, for example, causing mismatches between the chronology of hibernation and food availability, with consequences on female fitness.

**Chapter III. Rubbing behaviour of European brown bears: factors affecting rub tree selectivity and density:** Scent-mediated communication is the main communication channel in many mammal species. The brown bear carries out chemical communication, among other means, through scents deposited on marking (or rub) trees. In this chapter, rub tree selectivity of the brown bear in the predominantly deciduous forests of the Cantabrian Mountains was assessed. First, dendrometric and environmental characteristics of rub trees were compared with those of control trees. Then, the potential factors affecting the density of rub trees along survey routes on footpaths were analysed.

**Chapter IV. Visual marking in mammals first proved by manipulations of brown bear tree debarking:** The results of the previous chapter, in addition to other reasons, led to the suspicion that visual signalling is more widely employed by animals than previously thought. Since visibility of visual marks depends on their background, species living most of their time in dark conditions (e.g. nocturnal, twilight or forest animals) may rely on bright signals to enhance visual display. To confirm and describe this behaviour not previously reported, a manipulative experiment on the marking tree network has been performed.

**Chapter V. The influence of road networks on a large carnivore spatial distribution and habitat suitability in a human-modified landscape:** Here, effect of transport infrastructures on the spatial ecology of the Cantabrian brown bear in its range of distribution was analysed. Specifically, the topographic and landscape factors that determine the relative position of brown bears in front of different types of roads differentiated according to traffic intensity have been investigated. To this end, the role of visibility and different individual and seasonal variables that could play a determining role in the avoidance of road transport by brown bears have been taken into account. With the information derived from this analysis, the effect of the roads on the suitability of habitat for the brown bear within the study area has been evaluated through tools of species distribution models (SDMs), useful as a tool for conservation. and the management of this type of populations.

# *Chapter I*

# Denning in brown bears

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## SUMMARY

Hibernation represents an adaptation for coping with unfavourable environmental conditions. For brown bears *Ursus arctos*, hibernation is a critical period as pronounced temporal reductions in several physiological functions occur. Here, we review the three main aspects of brown bear denning: (1) den chronology, (2) den characteristics, and (3) hibernation physiology in order to identify (a) proximate and ultimate factors of hibernation as well as (b) research gaps and conservation priorities. Den chronology, which varies by sex and reproductive status, depends on environmental factors, such as snow, temperature, food availability and den altitude. Significant variation in hibernation across latitudes occurs for both den entry and exit. The choice of a den and its surroundings may affect individual fitness, e.g. loss of offspring and excessive energy consumption. Den selection is the result of broad- and fine-scale habitat selection, mainly linked to den insulation, remoteness and availability of food in in the surroundings of the den location. Hibernation is a metabolic challenge for the brown bears, in which a series of physiological adaptations in tissues and organs enable survival under nutritional deprivation, maintain high levels of lipids, preserve muscle and bone and prevent cardiovascular pathologies such as atherosclerosis. It is important to understand: (a) proximate and ultimate factors in denning behaviour and the difference between actual drivers of hibernation (i.e. factors to which bears directly respond) and their correlates; (b) how changes in climatic factors might affect the ability of bears to face global climate change and the human-mediated changes in food-availability; (c) hyperphagia (period in which brown bears accumulate fat reserves), predenning and denning periods, including for those populations in which bears do not hibernate every year; and (d) how to approach the study of bear denning merging insights from different perspectives, i.e. physiology, ecology, behaviour.

## INTRODUCTION

Hibernation is an important life history activity that coincides with winter in seasonal environments, and represents an adaptation for coping with harsh environmental conditions, generally associated with low temperatures and low food abundance (Geiser 2013; Ruf and Geiser 2015).

For brown bears *Ursus arctos*, hibernation is a critical period because at that time (Linnell et al. 2000; Friebe et al. 2001; Haroldson et al. 2002; Geiser 2004): (a) pregnant females give birth and undergo lactation while in dens; (b) energy savings during hibernation can be substantial; and (c) premature exit can negatively affect energy conservation and cub survival (Pigeon et al. 2016b). Thus, the conservation and management of brown bears requires knowledge regarding the denning ecology of different populations. Moreover, hibernation demands a preceding phase (hyperphagia) involving the intense search for food in order to store energy, and bears may spend as much as half of their life in winter dens (Friebe et al. 2001). Prior to hibernation, brown bears select specific denning sites as well as dens and, while in dens, bears show pronounced temporal reductions in several physiological functions and do not feed or drink (Hellgren 1998; Linnell et al. 2000). Finally, the choice of the brown bear as an interesting case study is based on two additional reasons: a) the existence of new research accumulated in the recent years on the hibernation of the species; and b) for being a species widely distributed around the northern hemisphere, with populations of different characteristics inhabiting very diverse habitats. This review thus allows identifying patterns or gradients of denning behaviour throughout the distribution range of the species and highlighting possible differences between populations.

Here, we review the three main aspects of brown bear denning, i.e. (1) den chronology, (2) den characteristics, and (3) hibernation physiology to provide an up-to-date assessment of this crucial phase of brown bear biology and to identify research gaps and conservation priorities during this life stage. When possible, we aimed to highlight commonalities and differences both within and among different bear populations and the underlying mechanisms. In particular, we expect that: (1) den chronology may vary by sex and bear reproductive status; (2) the duration of hibernation also depends on environmental factors, i.e. snow, temperature and food availability; (3) a relationship may exist between denning period and latitude, longitude and altitude; and (4) although the choice of a den and den surroundings may be variable, some differences may still exist by class, age and sex. Taking the opportunity to review a topic with a vast scientific literature, we also aimed to identify ultimate (i.e. factors which in the course of evolution have shaped, through natural selection, biological processes and behaviours) and proximate (i.e. external stimuli which initiate or maintain biological processes and behaviours) factors in denning behaviour, particularly regarding the behaviour of individuals of different reproductive categories, ages, sexes and populations. This approach will also allow for clarifying actual drivers, i.e. factors to which bears directly respond, and their correlates, i.e. factors that may be correlated to actual drivers.

## METHODS

The search for articles related to the theme of brown bear denning behaviour and hibernation was carried out until March 2020 using Google Scholar and Thomson Reuters 'Web of Science' (Scopus) databases. We conducted a literature review using a broad range of terms that represent the variety of ways in which bear denning behaviour and hibernation may be included. The terms ‘bear’, ‘grizzly’ and ‘*Ursus arctos*’ were combined with the following terms: ‘den’, ‘denning chronology’, ‘denning ecology’, ‘den entry’, ‘den exit’, ‘hibernation’, ‘hibernation driver’ and ‘phenology’. We also searched in the literature-cited section of all retrieved articles. We primarily selected studies conducted on free-ranging brown bears, which were organized according to the three main themes concerning hibernation: den chronology (n = 45 papers), den characteristics and surroundings (n = 42 papers) and physiology of hibernation (n = 61 papers). Finally, we added necessary references to complete the introduction and discuss the results (e. g. other hibernating mammals and Global Change). Possible variations in hibernation period across latitudes and longitudes for both den entry and exit where tested by Pearson’s correlations, while a Spearman correlation was used to test the relationship between den entry and exit with altitude.

# RESULTS

## A. Denning chronology

### A.1. Predenning period

After hyperphagia, during which bears accumulate the energy necessary for hibernation, individuals gradually decrease their rhythms of activity and movements before den entry (Friebe et al. 2001; Manchi and Swenson 2005; Sahlén et al. 2011). This phase, called predenning, which generally lasts between one and two weeks (Friebe et al. 2001; Manchi and Swenson 2005; Sahlén et al. 2011), may also go on for more than one month (Servheen and Klaver 1983; Evans et al. 2016). Alongside the decrease in activity, physiological changes occur during the predenning period (Evans et al. 2016).

This period may vary among the different categories and age classes of bears (Manchi and Swenson 2005; Sahlén et al. 2015b). For example, adult males and females with offspring generally arrive in denning sites after pregnant females, solitary females and females with cubs-of-the-year (Sahlén et al. 2011). Probably due to their greater experience and knowledge of their home range (Manchi and Swenson 2005), older bears seem to spend less time than younger individuals in the denning area before hibernation (Sahlén et al. 2011, 2015a). Finally, the length of the predenning period can also vary across years (Manchi and Swenson 2005; Sahlén et al. 2015a).

### A.2. Influence of sex and reproductive status

Similarly, den chronology also varies by sex and reproductive status (Figure 1), with females entering the den earlier and leaving later compared to males (Craighead and Craighead 1972; Judd et al. 1986; Schoen et al. 1987; Van Daele et al. 1990; Haroldson et al. 2002; McLoughlin et al. 2002; Ciarniello et al. 2005; Manchi and Swenson 2005; Pigeon et al. 2016b). Specifically, pregnant females enter the den earlier and exit later than other bear classes, the latter probably because of their need to spend more time inside the den to take care of new-born cubs, as well as the limited mobility of the cubs in the first weeks of life (Judd et al. 1986; Schoen et al. 1987; Van Daele et al. 1990; Friebe et al. 2001; Haroldson et al. 2002; McLoughlin et al. 2002; Ciarniello et al. 2005; Manchi and Swenson 2005; Graham and Stenhouse 2014; Pigeon et al. 2016b; Planella et al. 2019). Generally, the bear groups that enter hibernation dens few time after pregnant females are females with cubs and lone adult females (Van Daele et al. 1990; Friebe et al. 2001; Pigeon et al. 2016b). Finally, males and subadults seem to generally have shorter denning periods than adult females (i.e. parturient females, females with yearlings or solitary females) (Judd et al. 1986; Schoen et al. 1987; Van Daele et al.

1990; Haroldson et al. 2002; McLoughlin et al. 2002; Ciarniello et al. 2005; Manchi and Swenson 2005; Pigeon et al. 2016b; Krofel et al. 2017).

The earlier arrival at denning sites and longer hibernation of pregnant females compared to other bear classes may occur because the denning chronology of pregnant females is mainly determined by an ultimate reason, namely reproductive needs, whereas other bear classes are mostly governed by a trade-off between proximate (environmental conditions) and ultimate (metabolic dietary-related needs, energy conservation) factors.

### A.3. Influence of environmental factors

The duration of hibernation can also depend on (proximate) environmental factors, i.e. snow, temperature and food availability. As a general rule, the duration of hibernation in different brown bear populations seems to be conditioned by both snowfall/snow depth in autumn (Craighead and Craighead 1972; Friebe et al. 2001; Manchi and Swenson 2005; Akhremenko and Sedalishchev 2008) and snowmelt in spring (Schoen et al. 1987; Pigeon et al. 2016b). Snowfall can act as a major impetus to begin hibernation (Craighead and Craighead 1972; Reynolds et al. 1976; Servheen and Klaver 1983; Friebe et al. 2001; Manchi and Swenson 2005), with bears generally entering dens after first snowfall (Craighead and Craighead 1972; Manchi and Swenson 2005; Evans et al. 2016), although occasional snowstorms seem not to act as a stimulus for den entry (Judd et al. 1986; Van Daele et al. 1990). However, no significant correlations were detected between den entry/exit and snow depth (Judd et al. 1986; Delgado et al. 2018). Likewise, Bojarska et al. (2019) reported a probability of observations of bears negatively correlated with depth of snow cover.

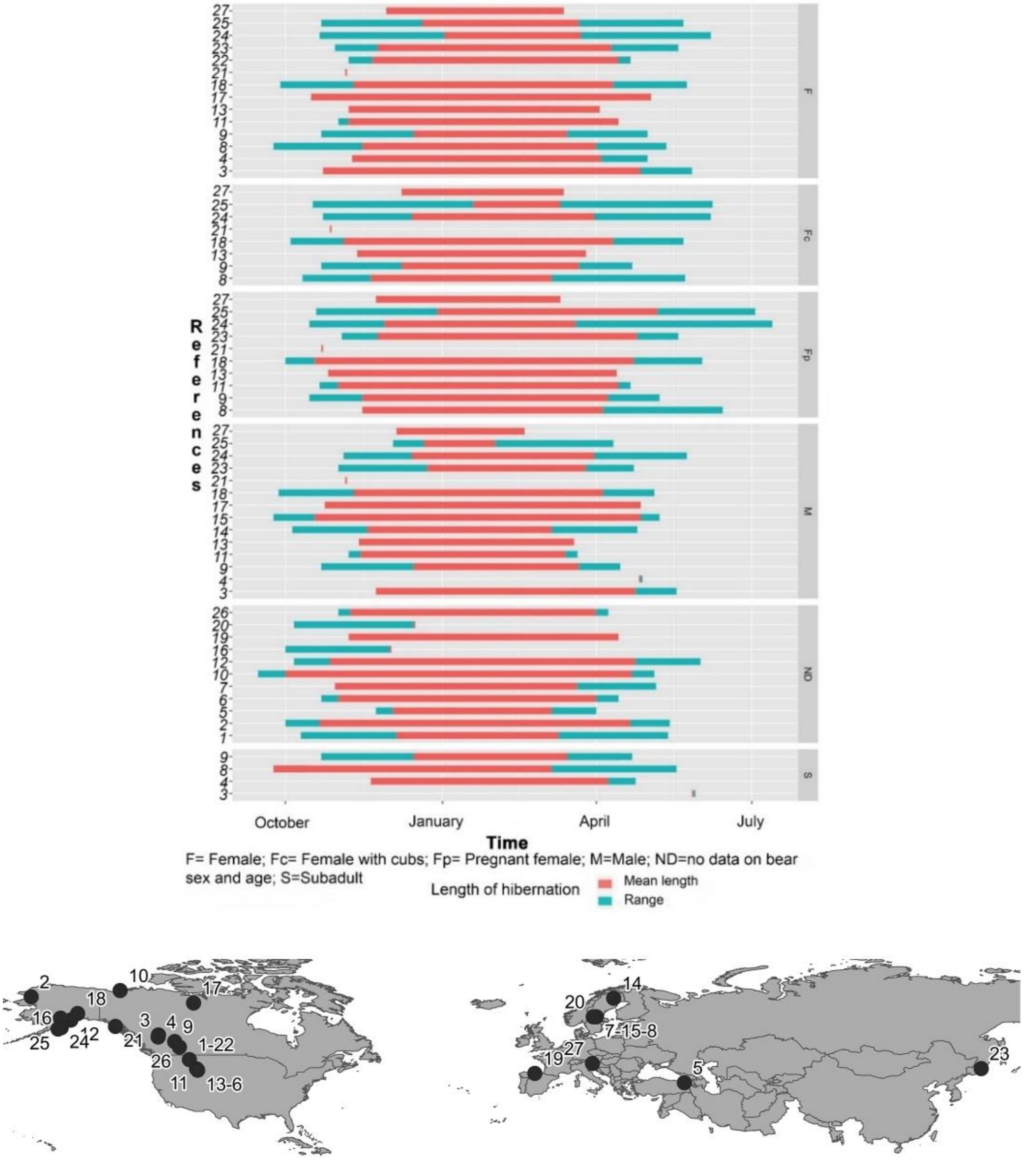

**Figure 1**. (A) Duration of brown bear hibernation by age class: F = female, Fc = female with cubs, Fp = pregnant female, M = male, S = Subadult, ND = no data available. Red lines represent the average duration of hibernation; cyan lines represent the first date of den entry and the last date of den exit. (B) Geographical locations of the areas in which the cited studies on the duration of brown bear hibernation have been carried out. References for the Figure 1**:** 1) (Aune 1994); 2) (Ballard et al. 1991); 3-4) (Ciarniello et al. 2005); 5) (Cozzi et al. 2016); 6) (Craighead and Craighead 1972); 7) (Evans et al. 2016); 8) (Friebe et al. 2001); 9) (Graham and Stenhouse 2014); 10) (Harding 1976); 11) (Haroldson et al. 2002); 12) (Hilderbrand et al. 2000); 13) (Judd et al. 1986); 14-15) (Manchi and Swenson 2005); 16) (Mangipane et al. 2018); 17) (McLoughlin et al. 2002); 18) (Miller 1990); 19) (Naves and Palomero 1993a); 20) (Sahlén et al. 2015a); 21) (Schoen et al. 1987); 22) (Servheen and Klaver 1983); 23) (Seryodkin et al. 2003); 24-25) (Van Daele et al. 1990); 26) (Vroom et al. 1980); 27) (Krofel et al. 2017).

Another important proximate factor affecting den entry/exit is ambient temperature (Craighead and Craighead 1972; McLoughlin et al. 2002; Manchi and Swenson 2005; Friebe et al. 2014; Evans et al. 2016; Pigeon et al. 2016b; Delgado et al. 2018). In Scandinavia, Evans et al. (2016) observed that the average (mean ± SE) daily temperature when bears enter dens is 1.03 ± 0.95°C, and that ambient temperature is associated with a decrease in body temperature which, consequently, results in a change in heart rate (Evans et al. 2016). When bears leave the den, the daily mean ambient temperature is 3.7 ± 1.3°C and their mean body temperature is 36.7 ± 0.15°C. A decrease in the length of the hibernation period and the postponement of den entry may be associated with warm winters (Evans et al. 2016), whereas low autumn temperatures may cause early den entry (Friebe et al. 2014). However, Pigeon et al. (2016b) considered that autumn temperatures may have a minor role in den entry dates. Some studies reported that den emergence might be somewhat regulated by temperature increase (McLoughlin et al. 2002; Manchi and Swenson 2005; González-Bernardo et al. 2020a), and Evans et al. (2016) showed that den exit was not dependent on the exact ambient temperature on the day of exit, probably because den emergence is a longer process in which physiology is tightly integrated with ambient temperature. In Poland, brown bear winter activity has been positively related to ambient temperature (Bojarska et al. 2019). However, brown bear sensitivity to changes in climatic conditions varies as a function of den entry and exit dates (Delgado et al. 2018). Indeed, brown bears are most sensitive to climatic variations around first exit and last entry dates, i.e. a change in ambient temperature in periods closer to the average date that bears first enter/exit their dens has a greater influence on denning dates than during other periods (Delgado et al. 2018).

The hibernation period is primarily affected by a decrease in food availability (Schoen et al. 1987; Van Daele et al. 1990; Pigeon et al. 2016b), which may also be related to the amount of snow (Pigeon et al. 2016b). Some authors have hypothesised that this snow-induced lower availability of food principally guides den entry and exit, i.e. the availability of food in late autumn-early winter delays den entry (Van Daele et al. 1990; Pigeon et al. 2016b). Food availability seems to affect less the den entry date of pregnant females, which start hibernating when berries are still available and abundant (Friebe et al. 2001), which supports the stronger dependence of pregnant females' hibernation on ultimate cues. Finally, because brown bears are facultative hibernators, the continuous availability of food and mild climate may prompt individuals to winter outside dens (Van Daele et al. 1990; Huber and Roth 1997; Nores et al. 2010).

### A.4. Influence of latitude, longitude and altitude

As a global pattern for brown bears, individuals in southern latitudes generally enter dens later and spend less time hibernating than bears in northern latitudes (Linnell et al. 2000; Haroldson et al. 2002; McLoughlin et al. 2002; Manchi and Swenson 2005; Graham and Stenhouse 2014) (Figure 2). When comparing different studies on den chronology, we detected a significant variation in hibernation period across latitudes for both den entry ($n = 57$, $r = -0.52$, $p = 0.0001$) and exit ($n = 59$, $r = 0.48$, $p = 0.0001$), with bears in more northern areas spending more time hibernating than bears in the southernmost latitudes (Figure 2). Proximate factors such as local weather conditions and the availability of food may be the drivers triggering the detected variations in den chronology. However, when taking into account the different classes of bears, i.e. adult males, adult females, females with cubs, pregnant females and subadults, den entry *vs*. latitude was only significant for adult males ($n = 12$, $r = -0.58$, $p = 0.05$) and nearly significant for adult females ($n = 14$, $r = -0.52$, $p = 0.06$). That is, for females with cubs, pregnant females and subadults, latitude seems to have only

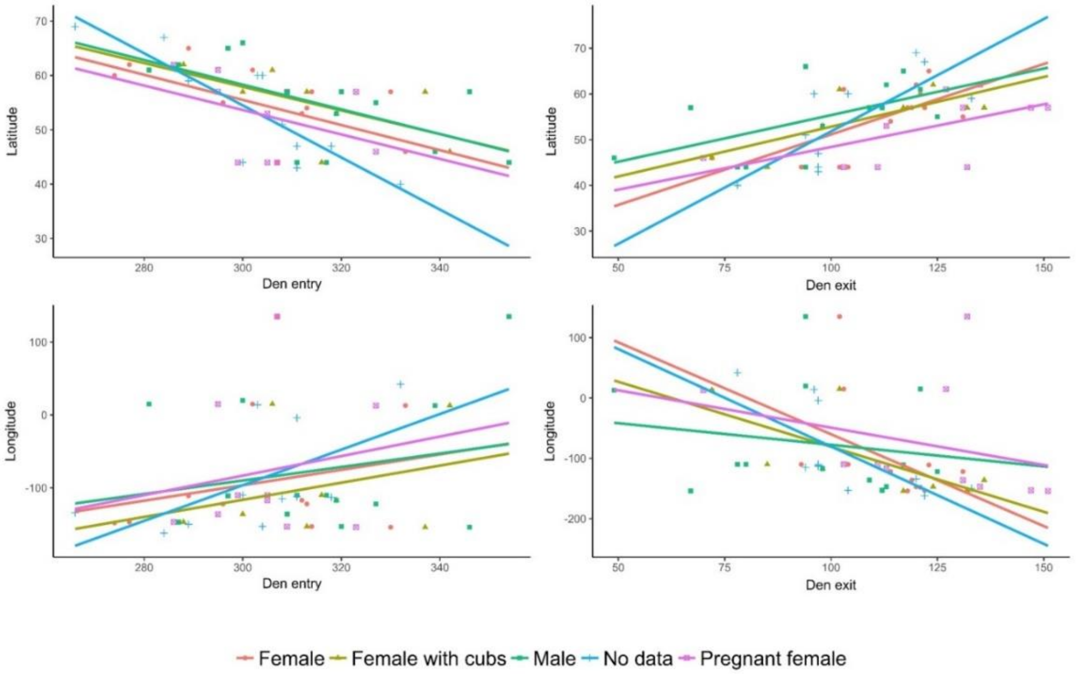

**Figure 2**. Dates of brown bear den entry and exit change according to latitude, longitude and age class. F = female, Fc = female with cubs, Fp = pregnant female, M = male, S = Subadult, ND = no age data available. References for the Figure 2**:** (Craighead and Craighead 1972; Lentfer et al. 1972; Vroom et al. 1980; Judd et al. 1986; Clevenger and Purroy 1988; Huber and Roth 1997; Groff et al. 1998; McLoughlin et al. 2002; Petram et al. 2004; Pigeon et al. 2016a).

a minor effect on hibernation length. On the other hand, when taking into account the different classes of bears for den exit *vs*. latitude, only adult females showed a significant correlation ($r = 0.68$, $p = 0.008$). Neither den entry ($r = 0.09$, $p = 0.51$) nor exit ($r = -0.21$, $p = 0.10$) were correlated with longitude (Figure 2). Den altitude may also affect the duration of hibernation because of the varying climatic conditions over altitudinal gradients (Ciarniello et al. 2005; Pigeon et al. 2016b), with bears denning at lower altitudes (e.g. plains, coastal areas) emerging earlier than those hibernating at higher altitudes. However, when comparing den chronology with the mean altitude of 8 study areas, neither den entry ($\rho = 0.10$, $p = 0.82$) nor exit ($\rho = -0.30$, $p = 0.47$) were significantly correlated with altitude.

## A.5. Den abandonment

Den abandonment, i.e. the premature leaving of a hibernation den with or without subsequent re-denning, has been reported in different populations of brown bears. Although den abandonment occurs naturally due to flooding or winter food availability (Schoen et al. 1987; Van Daele et al. 1990; Huber and Roth 1997; Nores et al. 2010), human activities have been reported as the main cause of den abandonment (Swenson et al. 1997; Linnell et al. 2000; Sahlén et al. 2015a). It has been reported how this effect is dependent on the distance at which human activity takes place (less than 1 km away and especially less than 200 m, den abandonment increases significantly Linnell et al. 2000). Thus, activities such as industrial and forestry activity, hunting (Swenson et al. 1997; Sahlén et al. 2015a), transit of people (Swenson et al. 1997) or even the research activity at the surroundings of the den (Huber and Roth 1997) have been described as causes of den abandonment. It has also been reported that abandoned dens were located at a shorter distance from roads than non-abandoned dens (Elfström and Swenson 2009). Different studies found that if den abandonment is due to disturbances it affects equally individuals of both sexes (Swenson et al. 1997; Krofel et al. 2017), while if it is due to the presence of a food source, a male-biased den abandonment (Van Daele et al. 1990; Krofel et al. 2017). Den abandonment can have negative consequences for populations (Linnell et al. 2000) as cub mortality increases (probability of losing at least one cub is multiplied by 10 in the case of den abandonment, Swenson et al. 1997).

Separate mention deserves the effect of the availability of food during the winter in the den abandonment. In certain populations where there are natural food sources during the winter, part of the population may not hibernate (males on Kodiak Island, Van Daele et al. 1990). This is more common in southern populations where weather conditions are less harsh and food is available permanently, such as hard mast or chestnuts (Clevenger et al. 1992) and where it is not unusual to see bears not hibernating or interrupting hibernation (Clevenger et al. 1990; Huber and Roth 1997; Nores et al. 2010). However, this food related den abandonment is especially intense in some populations where bears have access to supplementary food during winter, which may alter the chronology of hibernation or winter activity patterns (Cozzi et al. 2016; Krofel et al. 2017; Bojarska et al. 2019).

## B. Den characteristics and surroundings

The choice of a den and the landscape features of its surroundings may affect individual fitness (Pigeon et al. 2014, 2016a; Smereka et al. 2017). For example if a pregnant female is forced to change her den during the winter, due to human disturbance or poor thermal qualities of the den, this can result in the loss of her offspring (Linnell et al. 2000). Females seem to show greater fidelity to denning area than males, as the same male individual is able to choose different dens at distances up to four times greater than that of females, e.g. 1.7 *vs*. 7.8 km (Linnell et al. 2000), while dispersing subadults do not seem to show fidelity to denning area (Manchi and Swenson 2005). There is little or no reuse of the same den over successive years (Schoen et al. 1987; Ciarniello et al. 2005; Elfström and Swenson 2009), although natural cavities seem to be more reused than excavated dens because the latter have lower structural stability (Linnell et al. 2000).

### B.1. Den structure

The most common den types are those excavated in the ground or located inside natural caves (Linnell et al. 2000). However, bears can also use other types of dens such as depressions under rock shelters, nest dens (a nest of needles and branches or other materials deposited on the ground) and tree cavities (Elfström et al. 2008; Elfström and Swenson 2009; Štofík and Saniga 2012; Seryodkin et al. 2018; Tammeleht et al. 2019). A common bear den is generally composed of three compartments (Figure 3): (1) an entrance; (2) a tunnel that connects the entrance with the resting chamber; and (3) a chamber occupied by the nest, i.e. the zone where the bear gathers vegetative material to build a bed. Some structural parameters of dens, such as total length, tunnel length, chamber length and width, may vary considerably (Figure 3), which might be due to the properties of the soil in excavated dens and brown bear adaptability when choosing natural cavities. The small size of the den, compared to that of the bear, allows greater thermal stability, and this is especially notable for excavated dens (Craighead and Craighead 1972; Petram et al. 2004). Some authors have suggested that although the construction of the den is an innate behaviour programmed into the bear's genes, it may also be improved through experience acquired from the mother at the yearling stage (Craighead and Craighead 1972; Vroom et al. 1980; Petram et al. 2004). In addition, the features of the caves used by brown bears as dens do not seem the result of population-specific traditions (Chirichella et al. 2019). Den construction can take place in only a few hours (Friebe et al. 2001), although bears can begin to prepare the den 1-2 months before den entry (Craighead and Craighead 1972; Krechmar and Krechmar 1992).

### B.2. Den landscapes

The choice of landscape surrounding the den is highly variable and mainly depends on the habitats available in the bear's home range (Linnell et al. 2000; Ciarniello et al. 2005; Elfström et al. 2008). Den selection is primarily the result of both broad- and fine-scale habitat selection, mainly linked to den insulation, remoteness and the availability of spring food resources at den emergence (Pigeon et al. 2014, 2016a).

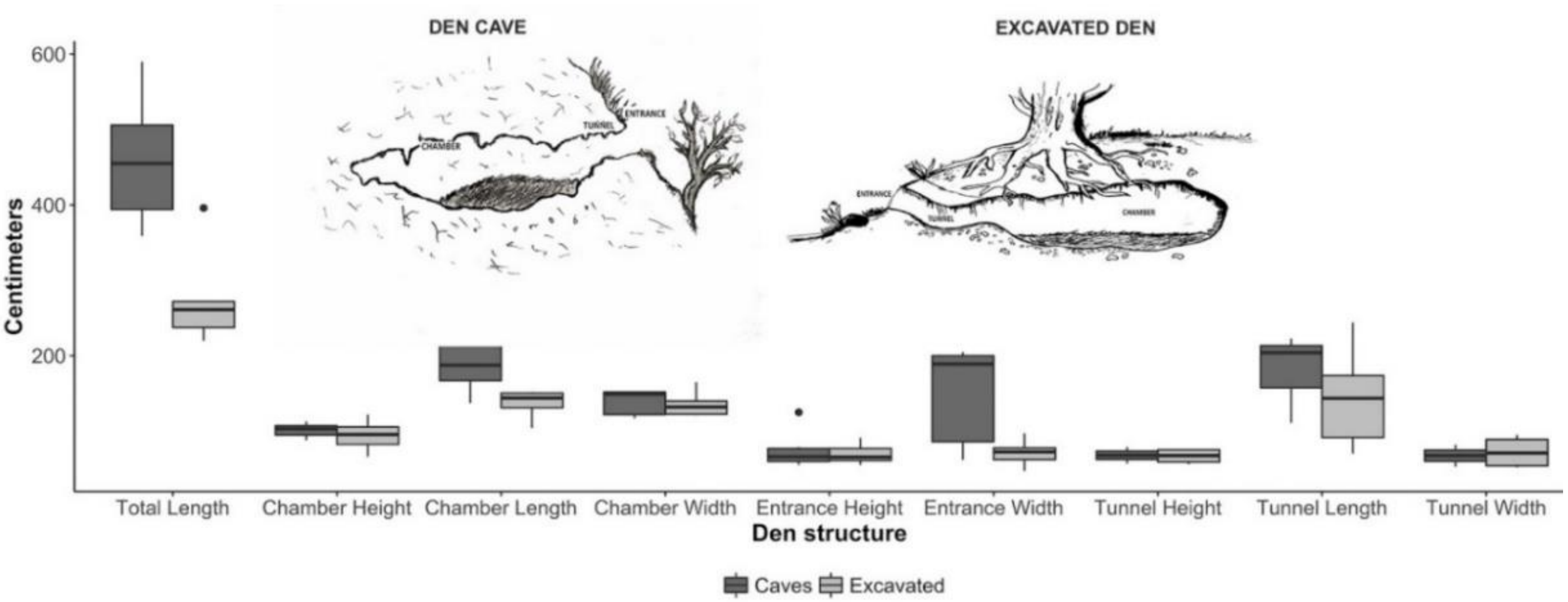

**Figure 3**. Dimensions (cm) of brown bear dens: excavated and natural caves. References for the Figure 3**:** (Craighead and Craighead 1972; Lentfer et al. 1972; Reynolds et al. 1976; Vroom et al. 1980; Judd et al. 1986; Schoen et al. 1987; Clevenger and Purroy 1988; Miller 1990; Huber and Roth 1997; Groff et al. 1998; Mcloughlin et al. 2002; Petram et al. 2004; Pigeon et al. 2016a; Krofel et al. 2017; Chirichella et al. 2019).

For example, the snowpack can have insulating properties that help maintain a constant temperature, and in this way decrease the energy cost to the animal as a result of thermoregulation (Lentfer et al. 1972; Reynolds et al. 1976; Vroom et al. 1980; Servheen and Klaver 1983; McLoughlin et al. 2002; Elfström et al. 2008; Libal et al. 2011). However, the role that snow might play when bears are inside the den is unclear. Thick forest cover may better protect dens from wind and cold temperatures (Pigeon et al. 2014, 2016a), and thick vegetation cover also guarantees concealment of the den entrance and, thus, protection from human disturbance (Sahlén et al. 2011; Chirichella et al. 2019). Finally, in the case of excavated dens, trees roots may help ensure greater structural stability of the den (Lentfer et al. 1972; Harding 1976; Vroom et al. 1980; Judd et al. 1986; Ciarniello et al. 2005; Smereka et al. 2017). In the case of excavated dens, brown bears also choose hibernation areas on the basis of lithological characteristics, selecting soils that not only are easier to dig but also increase den stability and insulating capacity (Harding 1976; Reynolds et al. 1976; Vroom et al. 1980; McLoughlin et al. 2002; Manchi and Swenson 2005; García et al. 2007; Smereka et al. 2017). Frequently, southeastern and southwestern slopes are preferred for greater insulation (Craighead and Craighead 1972; Harding 1976; Schoen et al. 1987; McLoughlin et al. 2002; Elfström et al. 2008; Štofík and Saniga 2012; Chirichella et al. 2019). Bears seem to prefer steeper slopes (Vroom et al. 1980; Servheen and Klaver 1983; McLoughlin et al. 2002; Ciarniello et al. 2005; Elfström et al. 2008; Goldstein et al. 2010; Libal et al. 2012; Štofík and Saniga 2012; Pigeon et al. 2014; Smereka et al. 2017; Sorum et al. 2019) which may allow for: (a) simpler digging of the den compared to flat ground (McLoughlin et al. 2002); (b) greater den structural resistance, reducing the likelihood of collapse (Vroom et al. 1980; Servheen and Klaver 1983; Ciarniello et al. 2005; Libal et al. 2012); (c) large amounts of radiant heat (Vroom et al. 1980; Ciarniello et al. 2005; Libal et al. 2012); and (d) better protection against disturbances (Naves and Palomero 1993a; Libal et al. 2011, 2012).

Den altitude varies from a minimum average height of 434 m a.s.l. to a maximum average height of 2696 m (n = 22 studies, see references in Supplemental File 2). However, brown bears seem to avoid denning in valley bottoms and high peaks (Linnell et al. 2000). Bears might also select dens at higher elevations given that: (a) greater altitude allows dens to be covered by more snow and, consequently, to have greater thermal insulation (Vroom et al. 1980; Libal et al. 2011, 2012; Whiteman et al. 2017; Eriksen et al. 2018; Sorum et al. 2019), in addition to having fewer melting-freezing events and better drainage (Whiteman et al. 2017; Eriksen et al. 2018); (b) dens at higher altitudes are further from the sources of human disturbance and are more inaccessible (Ciarniello et al. 2005; Pigeon et al. 2014; Whiteman et al. 2017; Chirichella et al. 2019); and (c) there are less natural predators, such as tigers (Seryodkin et al. 2003, 2018), at higher altitudes.

### B.3. Den selection and human disturbance

Humans may influence brown bear den selection (Craighead and Craighead 1972). Actually, human activities and infrastructures may determine denning locations, e.g. by increasing the distance from humans (Elfström et al. 2008; Elfström and Swenson 2009; Eriksen et al. 2018) and/or by forcing bear to select concealed or inaccessible places. For example, winter dens close to human settlements or infrastructures (mainly roads), are typically located on steep (Groff et al. 1998; Petram et al. 2004; Eriksen et al. 2018) and rugged (Sahlén et al. 2011; Eriksen et al. 2018) slope, as well as in areas with dense forest cover (Sahlén et al. 2011; Pigeon et al. 2014; Eriksen et al. 2018; Tammeleht et al. 2019). It has also been suggested that in places with a long history of persecution, such as Scandinavia, bears would select denning locations that are inaccessible or hidden (Eriksen et al. 2018).

### B.4. Den selection by class, age and sex

Den selection may also vary according to the different classes of bears, as well as age and sex. As a general pattern, females seem to prefer dens at higher altitudes and with steeper slopes (Schoen et al. 1987; Libal et al. 2011), and this is particularly true for pregnant females, probably because these areas allow for a longer period of denning as a result of favourable thermal conditions, i.e. longer snow cover at higher altitudes increases thermal insulation and reduces energy loss (Haroldson et al. 2002). In contrast, males may select areas at lower altitudes because of the greater availability of food at den emergence, which allows bears to rapidly increase body mass and thus improve breeding success (Libal et al. 2011). Yet, (1) females may also select areas within the tree-line (Gardner et al. 2014), (2) there are no differences between age classes in the selection of elevation and slope (Podruzny et al. 2002; Elfström and Swenson 2009), and (3) males can hibernate in areas at higher altitudes than females (Seryodkin et al. 2003). Thus, whereas proximate factors might be at the origin of den selection for most brown bear classes, ages and both sexes, pregnant females may select dens mainly on the basis of reproduction needs.

## C. Hibernation physiology and the potential energetic costs

Brown bears hibernate for several months during which they do not eat, drink, defecate or urinate, thus reducing the use of the bladder, kidneys and digestive tract (Folk et al. 1972; Hissa 1997; Stenvinkel et al. 2013a). Hibernation adaptations allow bears to overcome anuria, hyperlipidaemia and immobilization (Welinder et al. 2016), preserve muscles and bones avoiding osteoporosis or sarcopenia (Vestergaard et al. 2011; Fröbert et al. 2020) and prevent diseases such as metabolic syndrome, diabetes and cardiovascular pathologies (Arinell et al. 2012; Nelson and Robbins 2015; Fröbert et al. 2020). The physiological modifications that occur in bears during hibernation, and which are summarised below, might be the result of ultimate factors such as metabolic dietary-related needs and energy conservation, which brown bears have to deal with to survive the winter (Table 1).

Although hibernating ursids share some adaptations with some smaller hibernators (e.g. squirrels, marmots, hamsters and hedgehogs), such as storage and depletion of body reserves, lower metabolic rate, and body temperature during hibernation, many of the physiological changes of hibernating ursids are unique (Hellgren 1998; Nelson and Robbins 2015). For example, hibernating bears only experienced slight drop in body temperature (Hellgren 1998), compared to the greater body temperature drop of small hibernators (Carey et al. 2003; Nelson and Robbins 2015). The metabolic rate drops in all hibernating mammals, but the mechanisms of metabolic rate reduction have been suggested to be different in bears (Geiser 2004; Evans et al. 2016). Bears and small hibernators reduce cardiac output during hibernation from the active state, but the decrease is much greater in the latter (Nelson and Robbins 2015). Actually, during the hibernation bears remain in an alert state and are thus able to rapidly increase their heart rate and mobility (Hissa et al. 1994; Evans et al. 2012, 2016), against the nonresponsive hibernating state exhibited by small hibernators (Nelson and Robbins 2015). The hibernating induction trigger (HIT), a compound present in the blood, might initiate physiological and metabolic changes that lead to hibernation (Hissa et al. 1994; Hellgren 1998; Jørgensen et al. 2014; Welinder et al. 2016), although it has also been suggested than more than a single substance could trigger all these changes (Hissa 1997). For example, the sex hormone-binding globulin protein, which increases its concentration 45-fold during hibernation, might also help trigger hibernation (Welinder et al. 2016).

**Table 1.** Brown bear haematology and coded references that show increases, decreases or non-significant differences of different compounds. References for the Table 1**:** 1) (Halloran and Pearson 1972); 2) (Hissa et al. 1994) ; (3 (Mominoki et al. 1996); 4) (Barboza et al. 1997); 5) (Hissa et al. 1998); 6) (Vestergaard et al. 2011); 7) (Stenvinkel et al. 2013a); 8) (Revsbech et al. 2013); 9) (Revsbech et al. 2014); 10) (Græsli et al. 2015); 11) (Welinder et al. 2016); 12) (Sommer et al. 2016); 13) (Stenvinkel et al. 2018).

| **Haematological compounds** | ***Decrease during hibernation*** | ***Increase during hibernation*** | ***No significant variation between active period and hibernation*** |
|---|---:|---:|---:|
| *Glucose* | | 7 | |
| *Fructose* | 7 | | |
| *Urea* | 2, 1, 5, 4, 7 | | |
| *Creatinine* | | 2, 7, 10 | 4 |

| | | | |
|---|---|---|---|
| *Urea/Creatinine ratio* | 2, 4, 7 | | |
| *Uric acid* | 7 | | 4 |
| *Lactate* | | 8 | |
| *β-hydroxybutyrate* | | 2, 10 | |
| *Potassium* | | | 10 |
| *Phosphorus* | 7 | | |
| *Calcium* | | 5 | 7, 10 |
| *Magnesium* | | 10 | |
| *Vit. D2 and metabolites* | | 6 | |
| *Vit. D3 and metabolites* | 5, 6 | | |
| *D3/D2 ratio* | 6 | | |
| *Osteocalcin* | 6 | | |
| *Thyroxine (T4)* | 2 | | |
| *Triiodothyroxine (T3)* | 2 | | |
| *Thyrotropin (TSH)* | | | 2 |
| *β-endorphins* | 2 | | |
| *Parathyroid hormone (PTH)* | | | 5, 6 |
| *Aldosterone* | | 5 | |
| *Total plasma protein* | | 11 | |
| *Albumin* | | 7, 10, 11 | |
| *Haptoglobin* | | 3 | |
| *Total amino acids* | | | 7 |
| *Essential amino acids* | | | 7 |
| *Non-essential amino acids* | | | 7 |
| *Branched chain amino acids* | | | 7 |
| *Cystine* | | 2, 5 | |
| *Cysteine* | 9 | | |
| *Lysine* | | 5, 7 | |
| *Alanine* | | 5 | |
| *Methionine* | 7, 13 | 2, 5 | |
| *Taurine* | 5, 7 | | |
| *Arginine* | 5 | | |
| *Asparagine* | 5, 7 | | |
| *Leucine* | | | 5 |
| *Isoleucine* | | | 5 |
| *Threonine* | 7 | | 5 |
| *Valine* | | | 5 |
| *Histidine* | | 5, 7 | |
| *Phenylalanine* | | 5 | |
| *3-metylhistidine* | | 2, 4, 7 | |
| *Ornithine* | | 5 | |
| *Tryptophan* | | | 5 |
| *Glycine* | | | 5 |
| *Glutamine* | | 7 | |
| *Glutamic acid* | | 7 | |
| *Lipase* | | | 10 |
| *Kinase* | | | 10 |
| *Amylase* | 10 | | |
| *Lactate dehydrogenase* | 10, 12 | | |
| *Alanine transaminase* | 10 | | |
| *Aspartate deaminase* | 10 | | |
| *Alkaline phosphatase* | 10 | | |
| *γ-glutamyl transpeptidase* | 10 | | |
| *Glutamate dehydrogenase* | 10 | | |

### C.1. Energy consumption and changes in body mass and temperature

Hibernation requires a reduction of metabolic mechanisms with the consequent decrease in body temperature and consumption of O2. In hibernating bears, bradycardia results in a reduced volume of circulating blood and a lower rate of $O_2$ consumption (Folk et al. 1972), and the metabolic rate falls to approximately 27% of basal rates (captive brown bears, Farley and Robbins 1995). The metabolic cycle of brown bears, during which body mass variation occurs, can be divided into three stages: (a) gain of lean mass during spring, (b) accumulation of fat during hyperphagia, and (c) weight loss during hibernation (Nelson et al. 1983; Hilderbrand et al. 1999). Evans et al. (2012) reported an increase in body mass of around 40% during the pre-hibernation hyperphagia phase for brown bears in Scandinavia. The rate of weight gain, which can reach up to 4 kg·day$^{-1}$ (Hilderbrand et al. 1999), depends on the size of the individual and their diet. During hibernation, losses of body mass can vary among latitudes (Swenson et al. 2007b) and between sexes (Kingsley et al. 1983: 18% in males *vs*. 40% in females), these losses being higher in pregnant females due to childbirth and cubs rearing (Hilderbrand et al. 2000; Keay et al. 2018). Similar patterns were reported by Swenson et al. (2007), who compared winter weight losses between Scandinavian and Dinaric bear populations: weight loss varied between sexes and latitudes (26% males *vs*. 40% females in Scandinavia; 18% in both males and females in the Dinaric Mountains). The latitudinal variation has been suggested to be due to prolonged hibernation (Swenson et al. 2007), while the variations between sexes might be due to the frequency and duration of hibernation interruptions by males when food is available during winter (Van Daele et al. 1990; Krofel et al. 2017). In addition, differences across populations have been reported in the proportional body fat content and proportion of calories from fat, indicating certain plasticity according to seasonal food availability, reproduction and climate (Hilderbrand et al.

2018). The decrease in body temperature during hibernation ranges from 3-5° C with respect to the body temperature of the active state (Hissa 1997; Jansen et al. 2016) and begins on average 13 days before den entry, while its recovery begins 63 days before den emergency (61.4% of the average hibernation time already completed, South-Central Sweden Evans et al. 2016).

### C.2. Lipid metabolism

The accumulated fat prior to hibernation plays three roles: a) to supply the energy needs during hibernation, b) to insulate the body of the bear helping to keep its temperature stable, and c) to provide energy immediately after hibernation (Folk et al. 1972). Because hibernating brown bears maintain a fat-based metabolism for several months, they exhibit an increase in plasma lipids (Arinell et al. 2012). High concentrations of phospholipids and cholesterol may be due to the shrinking of the membrane of the adipocytes caused by dehydration (Welinder et al. 2016). The high concentrations of free fatty acids (FA) and glycerol might be the result of their release from adipose tissue during hibernation (Welinder et al. 2016), with short chain (easier oxidation) of FAs being released and retained in muscle and tissue adipose than long FA chains, as it occurs in other hibernating mammals (Giroud et al. 2019). Long chain of FAs, such as Omega 3 and Omega 6, some of which are responsible for carbohydrate metabolism and protein sparing in bear muscles (Chazarin et al. 2019a), vary their concentration in muscles and plasma differently between the active and hibernating states (Giroud et al. 2018). However, metabolites as eicosanoids decrease or do not vary their concentration during hibernation (regardless of their pro or anti-inflammatory properties), suggesting that the hibernation period is associated with a depressed state of the eicosanoid cascade (Giroud et al. 2018)Adiponectin is secreted exclusively in adipose tissue and is responsible for inducing insulin resistance to regulate the oxidation of fatty acids (Havel 2002; You et al. 2005), which may help maintain lipogenesis during the hyperphagia when bears need to store fat, whereas the decrease during hibernation that generates insulin resistance facilitates the switch to a lipolytic metabolism (Kadowaki et al. 2006). Leptin has a regulating function of appetite, so that increased serum concentration decreases food intake (Wang et al. 1997; Trayhurn et al. 1999). Some studies have described the temporary insensitivity of brown bears to leptin during hyperphagia, with a peak at the end of this period and, consequently, a sharp decrease in appetite at the moment of den entry (Nelson et al. 1983).

### C.2. Metabolism of nitrogenous substances and turnover of protein compounds

During hibernation, when bears do not excrete waste in the form of urine or excrement (Stenvinkel et al. 2013b), their bladder becomes permeable and both water and nitrogenous substances of the urine (such as urea) re-enter the blood (Brown et al. 1971; Nelson et al. 1975). Therefore, bear physiological adaptations allow recycling of nitrogenous substances, such as urea or creatinine, preventing the development of renal complications or azotaemia (Brown et al. 1971; Barboza et al. 1997; Stenvinkel et al. 2013b, 2018).

The urea content of blood plasma decreases during the hibernation period (Brown et al. 1971; Halloran and Pearson 1972; Hissa et al. 1994, 1998), being up to two times less than that outside hibernation (Stenvinkel et al. 2013a). It has been observed that urea decrease begins in autumn, probably due to a higher intake of fruits and berries, which are poor in protein (Welch et al. 1997). The mechanism by which hibernating bears reduces their urea levels is unique (Nelson et al. 1975; Stenvinkel et al. 2013b). It is based on a reduction of urea synthesis in the liver and its recycling by reincorporating urea into skeletal muscle and other proteins (Nelson et al. 1975;

Stenvinkel et al. 2018), and the possible conversion of part of the urea into ammonia and $CO_2$ by gut microbiota (Barboza et al. 1997; Hellgren 1998). This mechanism would have the added advantage of preventing the loss of muscle tissue during hibernation (Stenvinkel et al. 2018). Parallel to the decrease in urea levels, there is an increase in creatinine (Hissa et al. 1994; Græsli et al. 2015), which can more than double, as it cannot be eliminated given that it is not metabolized during hibernation and there is no excretion (Stenvinkel et al. 2013a). Thus, there is a change in the urea/creatinine ratio from the active period to hibernation (Hissa et al. 1994; Stenvinkel et al. 2013a). The synthesis of urea in the liver decreases as part of metabolic energy saving during hibernation (Stenvinkel et al. 2013a) and as a result of the change from a carbohydrate and protein metabolism to a lipid metabolism (Græsli et al. 2015).

Different studies have reported very different trends regarding the seasonal variations of plasma proteins and amino acids (Supplemental File 1). Despite not consuming any protein during the fasting that accompanies hibernation, the protein content of serum decreases little during this period (4-17%) (Chanon et al. 2018), and increases in the case of some proteins and amino acids (Supplemental File 1). Hellgren (1998) even suggested that increases in protein metabolism could (a) prevent its catabolism into carbon dioxide, water and urea, and (b) supply the needs of specific enzymes such as lipolytics, gluconeogenics or proteolytics.

### C.3. Response of the circulatory system to hibernation

A multitude of cardiovascular and haematological adaptations of the circulatory system occur during hibernation, many of them aimed at conserving energy (Jørgensen et al. 2014). Heart rate begins to decrease 24 days before den entry, whereas recovery of cardiac parameters starts 33 days before den exit (unanesthetized bears, South-Central Sweden Evans et al. 2016). However, despite the fact that brown bears (a) exhibit blood parameters that would be indicators of pathology in humans and (b) maintain levels of cholesterol and triglycerides much higher than healthy human values, atherosclerosis, fatty streaks, foam cell infiltration and inflammation have not been reported, and coronary artery examination has revealed the absence of atherosclerotic changes (Arinell et al. 2012). Deep bradycardia leads to a reduction in blood flow, which decreases the low shear stress in blood vessels, a factor that is related to atherosclerotic plaque (Jørgensen et al. 2014).

As a result of a decrease in metabolic rate and activity, hibernating brown bears exhibit marked bradycardia in which the heart rate decreases between 63 and 80% (unanesthetized bears: (Evans et al. 2016); anesthetized bears: (Folk et al. 1972; Nelson and Robbins 2010; Jørgensen et al. 2014, 2020)). However, blood pressure does not seem to change during hibernation (Nelson et al. 2003). Cardiac output has been reported as significantly lower during hibernation, representing only 24% of the active period value (0.86 *vs.* 3.54 $\mathrm{l \cdot min^{-1}}$). Another measure of cardiac activity, the cardiac index, is also lower in brown bears during hibernation, with a value nearly only a quarter (26%) of that for the active period (2.45 *vs.* 0.63 $\mathrm{l \cdot min^{-1} \cdot m^{-2}}$). Stroke volume also varies, decreasing ca. 69% during hibernation, which is consistent with adaptation to low energy demands (Jørgensen et al. 2014).

### C.4. Skeletal response to hibernation, bone turnover and changes in skeletal muscles

The periods of shivering experienced periodically by hibernating bears, which help maintain muscle function, may also generate skeletal loading on bone to preserve its properties (Lin et al. 2004). The concentration of the parathyroid hormone, which stimulates osteoclast activity and weakens bone by releasing $Ca^{2+}$ into the blood, does not vary significantly between summer and winter (Supplemental File 1), consistent with the similar levels of $Ca^{2+}$ in the blood between seasons (Hissa et al. 1998; Vestergaard et al. 2011; Stenvinkel et al. 2013a; Græsli et al. 2015). On the other hand, some authors described a two-fold lower concentration of osteocalcin (the hormone indicative of bone formation; Vestergaard et al. 2011) and a decline of alkaline phosphatase (the hormone related to bone formation) during hibernation (Græsli et al. 2015) . Brown bear bones do not lose their mechanical function despite inactivity (McGee-Lawrence et al. 2008). An increase in trabecular remodelling (the trabecular bone is formed of interstitial septa called trabeculae, forming a spongy structure) might allow for the maintenance of trabecular structure and $Ca^{2+}$ homeostasis, since bears cannot excrete the latter during hibernation (Floyd et al. 1990), and it is considered the main factor in maintaining bone health (Stenvinkel et al. 2018).

Brown bears show no noticeable loss of muscle function or marked atrophy during hibernation (Salmov et al. 2015). During hibernation brown bears experience shivering (McGee et al. 2008), with periods that can exceed an hour in duration where activations lasting less than 0.2 s and occur every 3–10 s. Shivering may stimulate skeletal muscles enough to maintain muscular fitness (captive brown bears, Lin et al. 2012). It has also been suggested that the plasma of hibernating bears has antiproteolytic properties, thus inhibiting muscle loss (Fuster et al. 2007; Salmov et al. 2015; Chanon et al. 2018), and that constant levels of prostaglandins in muscle could contribute to muscle sparing in bears (Giroud et al. 2018). Skeletal muscles in hibernating brown bears are alleviated from oxidative stress, through the increased expression of cold-inducible proteins, and from a reduced production of reactive oxygen species (due to metabolic suppression and increased activity of antioxidant systems), which would confer resistance to skeletal muscle atrophy (Chazarin et al. 2019b). The maintenance of glycolysis would contribute maintaining functionality in cases of rapid den exit and fast increase in ATP production (Chazarin et al. 2019a). Finally, higher levels of metabolic microRNAs during hibernation have been reported to be responsible for metabolic suppression and for the activation of myogenic pathways, decreasing atrophic signalling (Luu et al. 2020). Taken together, these findings suggest that brown bears are able to maintain both muscle mass and function by reducing catabolic processes and maintaining a certain level of mechanical activity.

### C.5. Liver and kidney changes during hibernation

Before fasting, anuria and decreased metabolic rate, organs involved in digestive, metabolic and excretion processes, such as the liver and kidneys, have their activity modified compared to the active period (Stenvinkel et al. 2013b; Græsli et al. 2015). Although the maintenance of circulating urea is indicative of a functioning liver during the hibernation of bears (Barboza et al. 1997), decreases in the levels of alkaline phosphatase (Græsli et al. 2015) (Supplemental File 1) and the concentration of bile acids occur (Lin et al. 2012), consistent with fasting and hypometabolism (Græsli et al. 2015; Sommer et al. 2016), a condition that has also been suggested for the pancreas due to the decrease in amylase concentration in serum (Græsli et al. 2015).

Perls-positive granules, indicative of the accumulation of stainable ferric iron, appear in the cytoplasm of Kupffer cells, as well as in other non-parenchymal cells and some hepatocytes, and central veins are partially pleated at den emergence, with the narrowest lumen diameters and portal veins partially fibrosed (Prunescu et al. 2003). This increase in Fe may be due to the inability of excreting it and weight loss, as Fe is phagocytized by the Kupffer cells without recycling to other organs, whereas the narrowing of the hepatic vessels may be due to the smaller volume of blood during hibernation, which may not be sufficient to preserve normal form and thus results in pleating.

The kidney has a reticulated structure with separate lobes that decrease resistance to intraluminal flow. A decrease of 90% in renal flow has been reported, indicating a decrease in function, due to the lack of water intake and a decrease of 50-70% in glomerular filtration rate (Stenvinkel et al. 2013a, 2018). Concentrations of urea and creatinine in the blood have been suggested as good indicators of renal function, and high values of these compounds could reflect impaired renal function (Stockham and Scott 2008). On the one hand, the very high concentrations of creatinine and magnesium in blood plasma (Supplemental File 1) (Hissa et al. 1994; Stenvinkel et al. 2013a; Græsli et al. 2015) have also been suggested as indicators of decreased function of the kidneys, since creatinine and magnesium are filtered from the blood by these organs (Græsli et al. 2015). On the other hand, although the glomerular filtration rate is reduced and the kidneys do not excrete during the hibernation process, serum urea decreases, indicating a unique ability of brown bears to recycle urea in protein compounds (Nelson et al. 1973).

### C.6. Pregnancy and lactation

Due to the difficulty of gaining access to free-ranging pregnant females and the invasive nature of their study in natural conditions, very few studies have been published on pregnancy and lactation in free-ranging bears. Therefore, the information that exists about these processes during hibernation in free-ranging brown bears is very scarce.

Brown bear females may go into heat from late spring to late summer (Lefranc et al. 1987; Fernández-Gil et al. 2006), and give birth during hibernation in mid-winter, around January-February, during a period when there is no intake of food and water (Farley and Robbins 1995). Although it has been suggested that the implantation of the blastocyst is delayed until den entry (Hensel et al. 1969), in one study conducted on free-ranging parturient females in Sweden, Friebe et al. (2014) found no correlation between the date of delivery and the den entry, suggesting the influence of factors other than the start of denning on blastocyst implantation. These authors report December 1 as the average implantation date and January 26 as the average date of parturition, with an average gestation duration of 56 days. This same study reports that body temperatures of pregnant females are higher during the gestation period than during the rest of hibernation, to then drop at parturition due to foetal development. In older females, as well as in females with high body fat content, (a) den entry dates and birth dates tend to be earlier than in other females, (b) the lactation period may be longer (Friebe et al. 2014), and (c) implant embryos and cub birth occur earlier. Females with high body fat content also produce more and better milk than lean mothers (Hissa 1997; Robbins et al. 2012; López-Alfaro et al. 2013). Finally, the mortality of cubs during the first summer is lower in females with a higher percentage of fat and lean mass (Keay et al. 2018).

## DISCUSSION

We suggest that ultimate factors, such as (a) circannual changes in climate, (b) metabolic dietary-related needs, (c) energy conservation (necessary for increasing the probability of survival despite limited food availability in winter) and (d) female pregnancy, over an evolutionary timescale, have shaped physiological mechanisms that make hibernation beneficial to brown bears. On the other hand, the main proximate factors of hibernation, which include current weather conditions and food availability, also contribute to triggering physiological mechanisms that initiate hibernation. Yet, there are several physiological correlates of hibernation that, along with the environmental conditions that trigger hibernation, may be considered proximate causes. Because proximate mechanisms that regulate hibernation are superimposed upon regulated circannual changes in appetite, body mass, reproduction needs and several physiological processes, it is important to correctly distinguish between actual drivers of hibernation, i.e. factors to which bears directly respond (temperature, snow, food availability) and their correlates, i.e. factors that may be correlated to actual drivers (physiological changes; (Carey et al. 2003)). However, since hibernation can be a flexible response, we suspect that the correlates of proximate factors might fluctuate according to current environmental variations.

Predicted variations in air temperatures generally point towards an increase in temperatures (IPCC 2013; Raftery et al. 2017), with a predicted increase of 2 to 4.9° C in global average temperature by 2100 (IPCC 2013). For example, the rise of mean temperatures, in addition to the increase in temperature and precipitation variability (Giorgi et al. 2004; Pendergrass et al. 2017), has already affected biological systems by altering the phenology of seasonal processes (Root et al. 2003). Inter-annual fluctuations in hibernation chronology are expected to occur due to inter-annual variations in climate, extreme climatic events and temperature anomalies resulting from climate change (Giorgi et al. 2004; Pendergrass et al. 2017). Moreover, the increased climatic variability could make the weather patterns that govern the seasonality of animal life cycles to some extent more unpredictable for many organisms, including bears (Weiskopf et al. 2020). Actually, these interannual fluctuations in hibernation chronology due to climatic conditions have already been reported in both American black bears (Miller et al. 2017) and brown bears (McLoughlin et al. 2002; Friebe et al. 2014; Evans et al. 2016; Pigeon et al. 2016b; Delgado et al. 2018). Pigeon et al. (2016b) reported that for each 4°C increase in spring temperature brown bear den exit occurs 10 days earlier. Thus, changes in climate could reduce the duration of hibernation in bears and lead to advanced den exit (Pigeon et al. 2016b; Johnson et al. 2017; Berman et al. 2019). It has been reported how brown bears emerge from winter dens when the ambient temperature reaches a certain level (3.7 ± 1.3 C in Evans et al. 2016), and since warmer springs may promote earlier first den exits (e.g. Delgado et al. 2018; González-Bernardo et al. 2020a), bears are expected to emerge from dens earlier as the climate continues to warm (Pigeon et al. 2016b; Johnson et al. 2017). . Although few data are available, it has been suggested that: (a) climate change may severely reduce the available spring food resources (Inouye et al. 2000; Holden et al. 2012; Roberts et al. 2014; Penteriani et al. 2019) or produce a temporary change in its availability (Deacy et al. 2017); and/or (b) if bears exit dens earlier, vegetation production may still not be sufficient to support their food requirements. This may be more important for populations that exhibit a lower altitudinal difference between denning and spring foraging habitat. Moreover, such increased mismatches might increase the likelihood of bear-human conflicts if bears emerge earlier and, thus, have fewer foraging options over a more protracted time. An increase in winter temperatures would have a negative effect on reproductive success and cub survival after den exit in brown bear populations: energy demands of hibernating mammals would increase with higher winter temperature, due to the increase of energetic costs of torpor (Humphries et al. 2002; Post and Forchhammer 2008; Turbill and Prior 2016; Albrecht et al. 2017). Moreover, it has been suggested that an early den exit might also have negative consequences on the physical condition of cubs at den emergence, and therefore their fitness, as cubs that leave prematurely may be smaller and thus more vulnerable to predation or infanticide (Bellemain et al. 2006; Pigeon et al. 2016b; Hertel et al. 2018). Thus, it is crucial to understand how changes in climatic factors might affect the ability of bears to cope with global climate change. Yet, understanding the relationship between hibernation and global warming is essential for brown bear conservation and management in a changing world as climate-induced changes in hibernation have the potential to affect individual and population fitness (Pigeon et al. 2016b; Delgado et al. 2018; Hertel et al. 2018).

Brown bears have been reported showing a noticeable plasticity when hibernating, adapting their denning behaviour to environmental factors, availability of food during hyperphagia or changing snow conditions during the winter (Fowler et al. 2019). However, it is unknown how adaptable brown bears can be to changes in food availability or climate regimes (Hertel et al. 2018). When this variability is predictable, as in populations where supplementary feeding is provided, populations have demonstrated a rapid adaptation of the hibernation chronology (Krofel et al. 2017; Bojarska et al. 2019). If these changes are less predictable, we lack information on how bears might adapt to these year-to-year fluctuations. Because (a) early den exit by females with cubs may have repercussions on the health of cubs (Bellemain et al. 2006; Pigeon et al. 2016b; Hertel et al. 2018), and (b) den abandonment of pregnant females increases probability of cub mortality (Swenson et al. 1997): (1) the autumn hunting season should end early enough so as to avoid disturbing female bears that have already denned or are showing predenning behaviour (Friebe et al. 2001; Lodberg-Holm et al. 2019), and (2) winter-early spring human activities should be minimized near suitable or traditional denning sites (Linnell et al. 2000).

It is important to highlight here the potential effect of anthropogenic food, and especially supplementary feeding, on the chronology of hibernation. Supplementary feeding of bears has several purposes including hunting, eco-tourism and the mitigation of human - bear conflicts (Penteriani et al. 2017, 2018). In areas where brown bears have access to anthropogenic food, shorter denning periods (over 50% reduction in denning period) or greater winter den abandonments than in populations located at a similar latitude where these food sources do not exist have been reported (Špacapan 2012; Krofel et al. 2017; Bojarska et al. 2019). Since supplementary feeding encourages bears to be active at an unusual time of year, one would also expect an increase in conflicts at a time of year when they are absent or less frequent. A decrease in the length of the hibernation period might also have unexpected and overlooked effects on bear physiology and behaviour. Thus, it is necessary to investigate the possible effects of supplemental feeding on denning behaviour.

Little information exists on the predenning stage, which is also important because individuals start to approach denning sites and seem to alter their movement patterns and rhythms of activity (Friebe et al. 2001; Manchi and Swenson 2005; Sahlén et al. 2011). Further research is needed on this phase which represents the link between hyperphagia and the moment of den entry.

In studies on denning, we risk focusing on correlated factors erroneously assuming they are true drivers, while we ignore the actual drivers. Clearly, it may prove to be difficult to distinguish between a true driver and its proxies, but insights from physiology might help in this regard, providing the opportunity for a unifying approach that merges insights from different perspectives and disciplines, i.e. physiology, ecology, behaviour. Also, it is very difficult to do these studies in the field; we rely on biologging and environmental data, often not even at the bear's den. As bears dens are not selected prior to denning, and the brown bear is extremely sensitive to disturbance, few researchers have data on environmental conditions at the den site (or in the den).

Finally, to our knowledge, almost no information exists on the hyperphagia, predenning and denning periods for those (southernmost and coastal) populations where hibernation does not occur every year and/or is only performed by part of the population or just some bear classes, e.g. pregnant females (but see Van Daele et al. 1990; Huber and Roth 1997; Nores et al. 2010; Krofel et al. 2017; Fuchs et al. 2019). Although brown bears are not obligate hibernators, hyperphagia and predenning are expected to prepare individuals to spend a considerable portion of their annual cycle in dens. Thus, information on movement patterns, rhythms of activity and the physiology of individuals that do not hibernate (or hibernate for short periods) may allow for useful comparisons with those brown bears that may spend up to six-month hibernating.

# *Chapter II*

# The role of spring temperatures in the den exit of female brown bears with cubs in southwestern Europe

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## SUMMARY

Hibernation represents the most refined adaptation of endothermic species to overcome unfavourable periods when food is scarce. Thus, hibernation should take place within specific time frames with respect to environmental factors. Flexibility in the timing of biological events is thus central to how well mammals can deal with varying climatic conditions. For brown bears (*Ursus arctos*), hibernation is not only a critical period that allows them to save vital energy reserves for times of food shortage, but also the period during which pregnant females give birth to cubs. Here, we analysed the relationship between 74 den exit dates of females with cubs, recorded from 1995 to 2018 in the Cantabrian Mountains in northwestern Spain, with (1) the average daily precipitation and (2) the average maximum temperature during the 30 days before den exit, as well as with (3) the number of cubs. The bears exited from 1 April to 16 May, and the mean date was 28 April. Our results, which are consistent with the general latitudinal pattern of den emergence reported in other studies, suggested that in years with higher maximum temperatures, exit dates tended to be earlier, whereas the number of cubs and the average rainfall for the 30 days prior to den exit did not seem to determine the variation in den exit dates. Considering the relationship between spring temperatures and the den exit dates of females with cubs, it is important to take into account the repercussions that the current global warming may have on the reproduction of brown bears. Current trends of climate change might trigger earlier den exit dates than in the past, which may have negative consequences on the population dynamics of brown bear populations. For example, a mismatch between the chronology of hibernation and food availability might reduce cub survival and, consequently, the fitness of females.

# INTRODUCTION

Hibernation is a vital strategy to survive unfavourable periods, such as times of food shortage and the adverse weather conditions of winter. In mammals, hibernation manifests as a temporary reduction in metabolism and physiological processes (Geiser 2004; Ruf and Geiser 2015; González-Bernardo et al. 2020b). Thus, this mechanism represents the most refined adaptation of endothermic species to overcome the cold season when food is scarce (Geiser 2013; Ruf and Geiser 2015). To be an adaptively efficient strategy, however, hibernation should be initiated and terminated within specific time frames in accordance with environmental factors. Flexibility in the timing of biological events is thus central to how well mammals can deal with varying climatic conditions (Mccain and King 2014; Gallinat et al. 2015).

For brown bears (*Ursus arctos*), hibernation is not only a critical period that allows them to save vital energy reserves for times of food shortage (Geiser 2004; Pigeon et al. 2016b), but also is the period during which pregnant females give birth to cubs in breeding dens and raise them during their first weeks of life (Ciarniello et al. 2005; Steyaert et al. 2012). In brown bears, gestation lasts an average of 56 days, with cubs born at the end of January (mean date: 26 Jan in Sweden; Friebe et al. 2014). Pregnant females are the cohort with the longest hibernation period among bears (Judd et al. 1986; Schoen et al. 1987; Miller 1990; Van Daele et al. 1990; Friebe et al. 2001; Haroldson et al. 2002; Ciarniello et al. 2005; Graham and Stenhouse 2014; Krofel et al. 2017). Accordingly, pregnant females, on average, tend to exhibit earlier den entry dates (Judd et al. 1986; Schoen et al. 1987; Friebe et al. 2001, 2014; Haroldson et al. 2002; Krofel et al. 2017) and later den exit dates than other bears (Van Daele et al. 1990; Friebe et al. 2001). It has also been suggested that females with cubs (hereafter, FCOYs) could also delay their exit from the den so that the cubs are better developed when they leave the den (Mcloughlin et al. 2002).

Dates of den entry and exit vary between different brown bear populations across the Northern Hemisphere because winters vary in duration and harshness according to latitude. Indeed, hibernation length generally shows a positive relationship with latitude (Haroldson et al. 2002; Manchi and Swenson 2005; Krofel et al. 2017) and brown bears have adapted their hibernation chronology to a series of environmental factors (Delgado et al. 2018; Fowler et al. 2019). Many studies have tried to identify the factors that might affect the chronology of brown bear hibernation and its duration, evaluating possible climatic, physiological, and food availability factors (Evans et al. 2016; Pigeon et al. 2016b; Delgado et al. 2018; Bojarska et al. 2019; Fowler et al. 2019). However, different drivers have been suggested for different bear populations; they appear to be area- or population-specific or both. Whereas some authors link the beginning of hibernation with food shortages (Schoen et al. 1987; Van Daele et al. 1990; Ciarniello et al. 2005; Pigeon et al. 2016b), others point to environmental factors, such as the first snowfall (Craighead and Craighead 1972; Manchi and Swenson 2005; Friebe et al. 2014; Evans et al. 2016; Delgado et al. 2018) or the temperature in autumn (Evans et al. 2016). With regard to the factors that determine den exit, negative relationships with the temperature during both winter (Evans et al. 2016) and spring (Miller 1990; Mcloughlin et al. 2002; Manchi and Swenson 2005; Pigeon et al. 2016b; Delgado et al. 2018) have been reported, in addition to positive relationships with snow depth and the date of snowmelt (Schoen et al. 1987; Fowler et al. 2019) as well as spring precipitation (Pigeon et al. 2016b). Additionally, human disturbances can force the change or premature abandonment of dens (Swenson et al. 1997; Linnell et al. 2000). Premature den abandonment can compromise population viability because it increases the risk of loss of cubs in pregnant females (Swenson et al. 1997) and decreases the survival rate of neonates

(Linnell et al. 2000).

Not all brown bears hibernate if they have food in winter (Van Daele et al. 1990), with this phenomenon being more commonly described in low latitudes, where winters are milder and snow cover less or ephemeral (Huber and Roth 1997; Nores et al. 2010). Likewise, a higher probability of observing brown bears during the winter has been reported as ambient temperature rises (Bojarska et al. 2019). Therefore, the factors that trigger the den exit of FCOYs might be more complex to understand than those that trigger den exit in the other categories of brown bears because pregnant females do not hibernate only as a result of food shortage. Understanding such factors is also important in the context of global warming, with current forecasts of increases of several °C by the end of the century at a global level (IPCC 2013; Raftery et al. 2017). The rise of mean temperatures (IPCC 2013), as well as the increase in temperature and precipitation variability (Giorgi et al. 2004; Pendergrass et al. 2017), has affected biological systems in part by altering the phenology of seasonal processes (Root et al. 2003), such as hibernation. Changes in climate could reduce the duration of hibernation in bears and lead to advanced den exit (Pigeon et al. 2016b; Johnson et al. 2017). For other hibernating mammals, such as rodents, the duration of hibernation (Inouye et al. 2000; Ozgul et al. 2010), as well as the fitness or survival rate of individuals (Turbill and Prior 2016), has been reduced in recent decades as a result of climate change. Climate change might also have negative consequences on the survival of cubs (Miller 1990; Pigeon et al. 2016b; Johnson et al. 2017) in particular, because an earlier den exit due to warmer temperatures implies smaller cubs, which might be more vulnerable to predation and infanticide (Sahlén et al. 2015b; Pigeon et al. 2016b) as well as possible mismatches with trophic resources (Inouye et al. 2000; Rodríguez et al. 2007; Bojarska and Selva 2012). Finally, an increase in winter temperatures has been shown to negatively affect reproduction of brown bears (Albrecht et al. 2017). On the other hand, a general increase in spring temperatures or rainfall could advance the availability of some foods, and an early den exit could thus be advantageous for brown bears to access these food resources (Fowler et al. 2019). In addition to the general trend toward an increase in temperature, interannual fluctuations in the chronology of hibernation may also be important. These fluctuations may be caused by both interannual variations in climatic variables resulting from climate change and extreme climatic events and temperature anomalies, which have been predicted for southwestern Europe (Giorgi et al. 2004; Castro et al. 2005; Pendergrass et al. 2017). These year-to-year changes in hibernation length have already been reported in American black bears (*U. americanus;* Miller et al. 2017) and even in brown bears, where these changes depend on temperatures or precipitation during winter and spring (Miller 1990; Mcloughlin et al. 2002; Friebe et al. 2014; Evans et al. 2016; Pigeon et al. 2016b; Johnson et al. 2017; Delgado et al. 2018). Therefore, identifying the triggers of den exit of FCOYs and its adjustment to climatic factors is of great importance and would allow for better predicting the effect of climate change on this vulnerable brown bear population.

Here, we analysed data on den exit dates of FCOYs collected over 19 years (from 1995 to 2018) for the small and isolated brown bear population inhabiting the Cantabrian Mountains (northwestern Spain), with the aim of exploring the attempt of bears to adjust their den exit to short-term variation in climatic conditions (which may be at least partially extracted from year-to-year variation), and assess the potential role of (1) temperature and rainfall, as well as (2) the number of cubs, in den exit dates. We also compared exit dates of the Cantabrian population with other studies carried out across the brown bear distribution area. Thus, we tested 3 main hypotheses: (1) higher temperatures in the month prior to den exit (when hibernating brown bears seem to be most sensitive to changes in temp; Delgado et al. 2018) will lead to earlier exit dates; (2) den exit will occur later if there are heavy rainfalls, which may represent harsh weather conditions for cubs; and (3) more cubs per litter will require greater energy demands that can be satisfied by an earlier den exit. To our knowledge, this is the first long-term study on den exit chronology carried out on FCOYs of one of the southernmost (42–43°N latitude) populations of brown bears.

# METHODS

## Study area

In this study, we considered most of the range currently occupied by brown bears in the Cantabrian Mountains (Figure 1), which consists of approximately 4,476 $km^2$ across parts of Asturias, León, and Palencia provinces (northwestern Spain; Penteriani et al. 2019). The Cantabrian Mountains are one of the main mountain systems in Spain and extend for approximately 300 km parallel to the Atlantic coast. Average altitude is approximately 1,100 m above sea level (a.s.l.), with the highest peak reaching 2,648 m a.s.l. (Martínez Cano et al. 2016). The region is characterized by an oceanic climate, with remarkable differences between northern slopes (oceanic climate with greater rainfall and more constant temperature) and southern slopes (continentalized and drier climate, with greater thermal amplitude, cold winters, and warmer summers; Ortega and Morales 2015). The landscape is mainly composed of forests (39%), shrubs (24%), and croplands (22%; Mateo-Sánchez et al. 2016), and the region is home to the largest extent of deciduous Atlantic forest in the Iberian Peninsula (Polunin and Walters 1985). Southern slopes are dominated by forests of semi-deciduous oaks and evergreen oaks (*Quercus pyrenaica* and *Q. ilex;* Mateo-Sánchez et al. 2016), whereas northern slopes are primarily occupied by deciduous forests of beeches (*Fagus* *sylvatica*), deciduous oaks (*Q. robur* and *Q. petraea*), birches (*Betula* spp.), and chestnuts (*Castanea sativa;* Mateo-Sánchez et al. 2016) with an understory mainly consisting of bilberry (*Vaccinium myrtillus;* Pato and Obeso 2012). Shrubs occur in degraded or non-forest areas, where several species of heather (*Erica, Calluna*) and brooms (*Genista, Cytisus*) predominate, among others (Fernández-Gil et al. 2006; Mateo-Sánchez et al. 2016). Above the tree line, around 1,500–1,700 m a.s.l., bilberries (*V. myrtillus V. uliginosum*), bearberries (*Arctostaphylos uva-ursi*), subalpine juniper (*Juniperus communis*), and buckthorns (*Rhamnus alpina*) are common (Pato and Obeso 2012; Martínez Cano et al. 2016). In general, the study area is characterized by a human-modified landscape, with core areas of optimal habitat inhabited by bears surrounded by a matrix of urbanized and cultivated areas with a high density of transport routes (Mateo-Sánchez et al. 2016; Zarzo-Arias et al. 2018, 2019). The predominant economic activity is the extensive breeding of livestock, followed by mining, timber harvest, and recreational activities such as tourism and hunting (Fernández-Gil et al. 2006).

## Brown bear data

We used information on the approximate date of 74 den exit events (defined as the first observation of a FCOY around the breeding den), number of cubs per den exit event, and den location in the Cantabrian Mountains collected from 1995 to 2018. We define den exit or den emergence as the time when the female leaves the winter den accompanied by cubs. The approximate date of den exit was obtained from (1) almost daily direct observations of den areas by rangers of the regional administrations (Principado de Asturias and Castilla y León, principally by the Patrulla Oso; i.e., Bear Patrol, in both regions), as well as by personnel of the Asturian Foundation for the

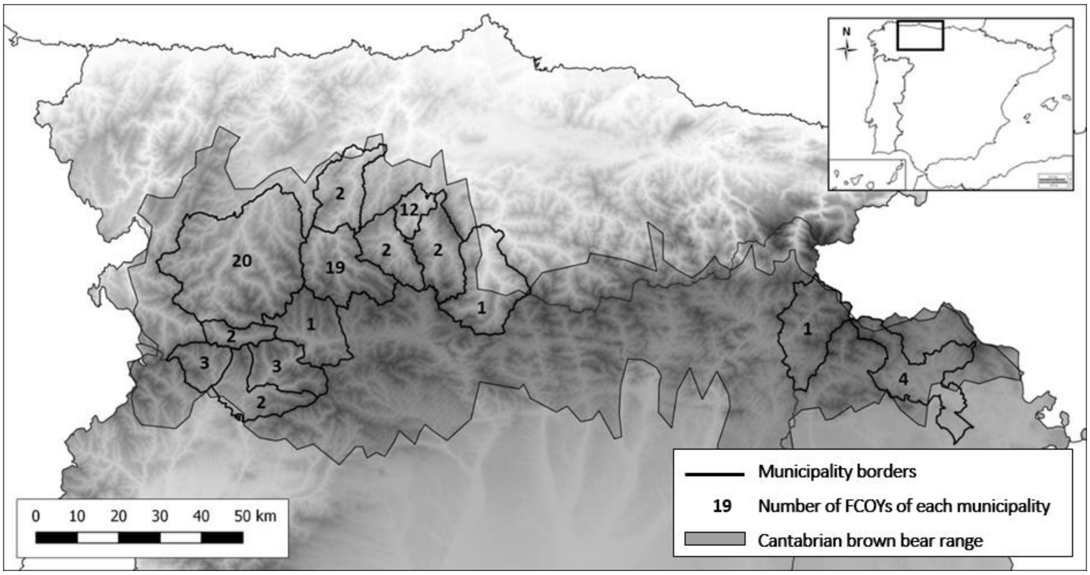

**Figure 1.** The distribution range of brown bears (*Ursus arctos*) in the Cantabrian Mountains (northwestern Spain; shaded area), together with the number of recorded dates of den exit (*n* = 74) of females with cubs (FCOYs) per municipality. The grey scale of the base map indicates the altitude of the terrain, with the darkest tones corresponding to areas of higher altitude.

Conservation of Wildlife (Fondo para la Protección de los Animales Salvajes), the Fundación Oso de Asturias, and the Brown Bear Foundation (Fundación Oso Pardo); and (2) almost daily personal observations by the authors. Indeed, every year, known reproductive den areas are intensively monitored from the beginning of spring (late Mar–beginning of Apr). Continuous and early monitoring of known breeding dens and their visibility (breeding dens in the Cantabrian Mountains are generally located in rocky areas with sparse vegetation, where bear families are visible; Zarzo-Arias et al. 2019a; Penteriani et al. 2020d and Supplemental Material) reduced the risk of considerable delay in the observation of FCOYs after den exit. Moreover, monitoring generally occurred during the 3 peaks of activity of females with cubs (i.e., around sunrise, between 12:00 and 15:00 hr, and at sunset [authors' unpublished data]). We considered the 16 May to be the last occurrence of den exit of a FCOY. After this date, the following first observations of females with cubs were too late (end of May–beginning of Jun) to be included as real den exits. However, this does not mean that some later den exits by FCOYs might not occur sporadically in the Cantabrian Mountains.

## Meteorological data

We collected data on average (1) daily precipitation and (2) maximum temperature for the 30 days before the first observation of each FCOY after den exit (i.e., when hibernating brown bears seem most sensitive to changes in temperature (Delgado et al. 2018). We did this for all FCOYs and for each of the years studied. This information was collected at the meteorological station closest to the den area (1–30 km) among the available stations administered by the Spanish State Meteorological Agency (Agencia Estatal de Meteorología) spread across the Cantabrian Range. We then calculated the mean of the collected maximum temperature and mean precipitation data. Similar studies carried out in other regions of the world (Evans et al. 2016; Pigeon et al. 2016b; Delgado et al. 2018) also included depth and permanence of snow cover, but we did not collect this information because snow cover is scarce or absent around breeding dens, especially in the month prior to first observations of FCOYs. The average number of days of snowfall in the study area is 38 and they are concentrated from December to March (Nores et al. 2010).

## Statistical analyses

Our sample size was relatively small to allow us to include all predictors into a single model, and we had, a priori, clearly distinct hypotheses. Therefore, we ran 2 separate statistical analyses. First, we were interested in assessing if the number of cubs of the year affected the den exit date of mother bears. To this end, we built a linear mixed model (LMM) with a normal distribution with Julian exit date as the response variable and the number of cubs as the explanatory variable. Second, we assessed which climatic factors are the most relevant for bear den exit. Such information may be at least partially extracted from year-to-year variation, which is likely to reflect the attempt of bears to adjust their phenology to short-term variation in climatic conditions. With such an aim, we employed a 2-step approach. First, we built 3 different LMMs using (1) den exit date (Julian date), (2) maximum temperature, or (3) precipitation for the 30 days before den exit as the response variable and year as the explanatory variable. We extracted the residuals of these models, which respectively represent shift-corrected phenological and shift-corrected climatic variables. We then built linear models to explain shift-corrected dates by shift-corrected climatic variables. There was no correlation between the 2 explanatory climatic variables ($r$ = 0.38, variance inflation factor, VIF = 1.17). In all models, we included the council in which each FCOY was located as a random factor to account for the fact that different bears were observed over different years in the same councils (i.e., repeated measurements) and the fact that the number of observed bears across years in the different councils were not the same (i.e., unbalanced data). We selected the best competing model or set of models based on Akaike's Information Criterion ($AIC_c$) and considered models with a $\Delta AIC_c$ value <2 as equally competitive. We also calculated values of $\Delta AIC_c$ and weighted $AIC_c$ of each competing model (Table 1). We ran all statistical analyses in Program R v. 3.5.1 statistical software (R Core Team 2018). We built linear models were built using the “lme4” package (Bates et al. 2015). We generated models and calculated $AIC_c$ values using the “dredge” function in the “MuMIn” package (Bartoń 2013).

**Table 1.** Comparison of the competing models built to analyze the effect of climatic variables (i.e., residuals of maximum temperature and precipitation for the 30 days before the first observation of brown bear [*Ursus arctos*] females with cubs on their den exit date in the Cantabrian Mountains, northwestern Spain, recorded from 1995 to 2018) based on values of $AIC_c$, $\Delta AIC_c$, and $AIC_c$ weights (*n* = 74 den exit events). Competitive models are ranked from the lowest (best model) to the highest $AIC_c$ value. Summary of fitted parameters is shown for models with $\Delta AIC_c < 2$. Conditional $R^2 = 0.18$.

| ***Competing models*** | | ***β*** | ***SE*** | ***$AIC_c$*** [a] | ***$\Delta AIC_c$*** [b] | ***$AIC_c$ weights*** |
|---|---|---|---|---|---|---|
| Max. temp | | | | 576.8 | | 0.649 |
| | Intercept | 0.147 | 2.141 | | | |
| | Max. temp | −1.319 | 0.475 | | | |
| Max. temp + Precipitation | | | | 579.1 | 2.27 | 0.208 |
| NULL | | | | 580.5 | 3.67 | 0.103 |
| Precipitation | | | | 582.4 | 5.58 | 0.040 |

[a] $AIC_c$ = Akaike Information Criterion, adjusted for small sample sizes.

[b] $\Delta AIC_c$ is the difference in $AIC_c$ value from the minimum $AIC_i$ model.

## RESULTS

Mean den exit date of FCOYs was 28 April in non-leap years (SD = 11.9 days). Most of the den exit dates were distributed toward the end of the range of dates. Only 19% (*n* = 14) of FCOYs left the den during the first half of April, and the remaining 32% (*n* = 24) and 49% (*n* = 36) of FCOYs left the den during the second half of April and the first half of May, respectively. When comparing our results with those obtained in other studies (Table 2), both the range and average den exit date correspond to the period of den exit for FCOYs of brown bear populations at similar latitudes. Our results seem to be consistent with the general latitudinal pattern of advancement of brown bear den exit as a function of decreasing latitude (Table 2).

**Table 2.** Den exit dates and hibernation lengths of brown bear (*Ursus arctos*) females with cubs for populations at different latitudes. Data are sorted by decreasing latitude of the study area. '-' indicates no data.

| **Study area** | **Latitude range** | **Mean date of den exit** | **Range of den exit** | **Mean hibernation length (days)** | ***N*** | **Source** |
|---|---|---|---|---|---|---|
| Norbotten (North Sweden) | 67–68°N | - | - | 226 | 15 | Manchi and Swenson 2005 |
| Talkeetna Mountains (South-central AK, USA) | 62–63°N | 15 May | 23 Apr–2 Jun | 217 | 16 | Miller 1990 |
| Dalarna (Central Sweden) | 61–62°N | 7 May | 5 Apr–14 Jun | 196 | 47 | Friebe et al. 2001 |
| Chichagof and Admiralty islands (Southeast AK, USA) | 57–58°N | 11 May | 1st week April–3rd week June | 211 | 18 | Schoen et al. 1987 |
| NE Kodiak Island (Southwest AK, USA) | 58°N | 27 May | 20 Mar–13 Jul | 211 | 15 | Van Daele et al. 1990 |
| SW Kodiak Island (Southwest AK, USA) | 57°N | 31 May | 7 May–3 Jul | 198 | 18 | |
| Mountains of Parsnip River area (BC, Canada) | 54–55°N | - | - | 206 | 6 | Ciarniello et al. 2005 |
| Plateau of Parsnip River area (BC, Canada) | 54–55°N | - | - | 177 | 3 | |
| Jasper National Park and the Wilmore Wilderness area (AB, Canada) | 53–54°N | 4th week April | 2nd week April–2nd week May | 175 | 17 | Graham and Stenhouse 2014 |
| Mission and Rattlesnake Mountains (MT, USA) | 47–48°N | 25–26 Apr | - | - | 1 | Servheen and Klaver 1983 |
| Sikhote-Alin State Biosphere Zapovednik (Russian Far East) | 44–45°N | 9 May (mean) | 25 Apr–19 May | 176 | 3 | Seryodkin et al. 2003 |
| Greater Yellowstone Ecosystem (MT, WY, and ID, USA) | 44–45°N | 3rd–4th week April | 4th week of March–3rd week May | 171 | 35 | Haroldson et al. 2002 |
| Yellowstone National Park area (MT, WY, and ID, USA) | 44–45°N | 13 Apr | - | 170 | 9 | Judd et al. 1986 |
| Dinaric Mountain Range (Slovenia) | 44–45°N | 11 Mar | - | 94[a] | 4 | Krofel et al. 2017 |
| Cantabrian Mountains (northwestern Spain) | 42–43°N | 28 Apr | 1 Apr–16 May[b] | - | 74 | This study |

[a] Supplementary feeding was provided to the brown bears of this study.

[b] To avoid potential bias due to late first observations of females with cubs from unknown dens, we considered 16. May to be the last den exit occurrence. However, this does not mean that some later den exits by FCOYs might not occur in the Cantabrian Mountains

We did not find any relationship between den exit dates and the number of cubs ($F_{1, 72}$: 0.25, $P$ = 0.62). Moreover, even though there was no significant trend in the exit date of FCOYs across study years, both den exit date and climatic variables (i.e., max. temperature and precipitation) showed year-to-year variability during the study period (Figure 2). Models built to assess the effect of this year-to-year climatic variation on the year-to-year variation of den exit revealed that only maximum temperature played a role in explaining the short-term fluctuations in den exit date (conditional $R^2$ = 0.18; Table 1). Specifically, our results showed that in years with higher spring temperatures, den exit dates of FCOYs were earlier.

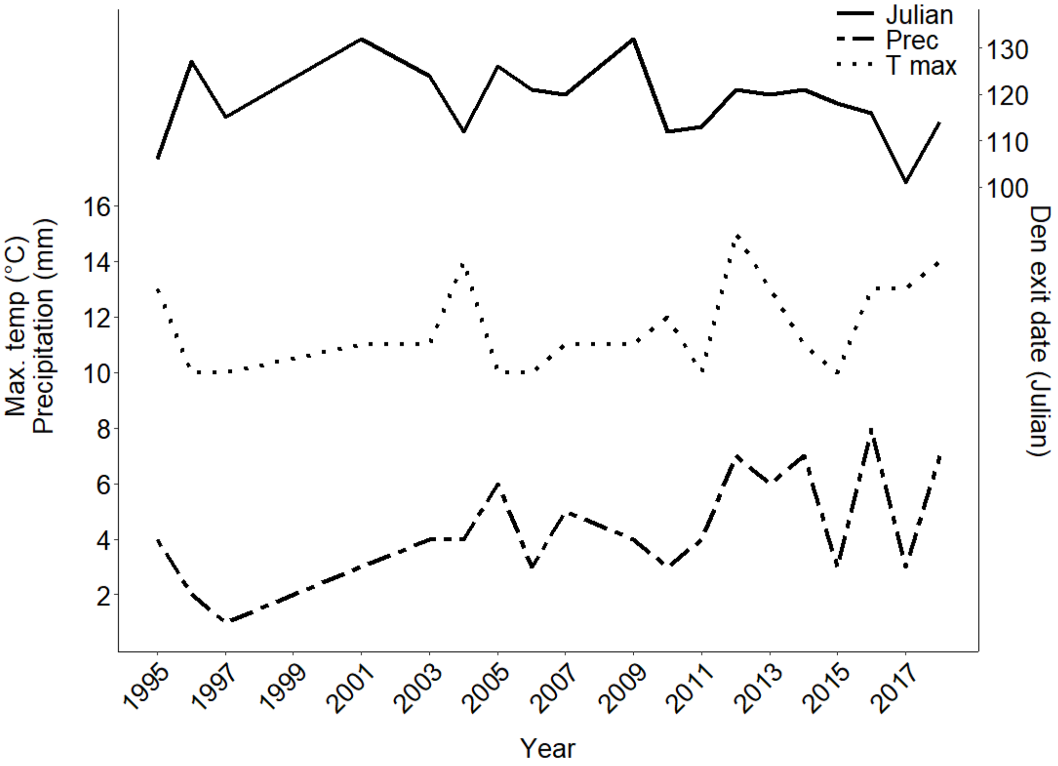

**Figure 2.** Annual variation in den exit dates (Julian dates, $n$ = 74) of female brown bears (*Ursus arctos*) with cubs in the Cantabrian Mountains, northwestern Spain, recorded from 1995 to 2018. Annual patterns of maximum temperature and precipitation in the 30 days prior to den exit are also shown.

## DISCUSSION

Brown bears show remarkable plasticity when hibernating, being able to adapt their denning behaviour to environmental factors, such as food available during hyperphagia or snow conditions during the winter (Fowler et al. 2019). In fact, the chronological variability of hibernation has been described as more intense as one moves away from the equator (Manchi and Swenson 2005; Fowler et al. 2019). In addition, previous studies that have analysed dates of brown bear den exit (Table 2) have shown that, generally, the average duration of hibernation decreases with distance to the equator (i.e., earlier dates of den exit), probably because of the reduced harshness of climatic conditions and greater availability of food in late autumn–early winter at more southerly latitudes (Manchi and Swenson 2005). Fowler et al. (2019) attributed this pattern to a stronger effect of the factors that determine the variability in hibernation at high latitudes, and Krofel et al. (2017) calculated an increase of 3.1 days in the duration of hibernation for each degree of north latitude. The range of the Cantabrian brown bear population is between 42° and 43°N latitude (i.e., within the southern limits of brown bear populations in Europe, along with those of the Pyrenees and the Balkan Peninsula). Following the patterns observed by Manchi and Swenson (2005) and Fowler et al. (2019), the dates in den exit recorded for the Cantabrian brown bear population are among the earliest dates reported for the species.

The mean date obtained for all FCOYs (last week of April) and the range of dates on which den exit occurs (from the first week of April to the second week of May) correspond to the exit dates we would expect according to the latitude of our study area (Table 2). Comparable exit dates have been recorded in 2 areas at latitudes similar to those of the Cantabrian Mountains (Yellowstone National Park in the USA [Judd et al. 1986,Haroldson et al. 2002] and Sikhote-Alin State Biosphere Zapovednik in the Russian Far East, [Seryodkin et al. 2003]). In addition, (Table 2), Haroldson et al. (2002) reported 1) a range of dates for den exit very similar to ours (i.e., from the fourth week of March to the third week of May); and 2) mean den exit between the third and fourth weeks of April, a date range that includes our mean den exit date (28 Apr).

The inverse relationship between maximum temperature and den exit in brown bears was also reported by Miller (1990), Mcloughlin et al. (2002), Manchi and Swenson (2005), and Delgado et al. (2018), as well as for American black bears by Miller et al. (2017) and Johnson et al. (2017). In particular, Pigeon et al. (2016) reported that for each increase of 4°C in spring temperature, den exit occurs 10 days earlier. Schoen et al. (1987) and Fowler et al. (2019) suggested that variation in the chronology of brown bear hibernation may also be due to snowpack or the timing of snowmelt; however, it has also been suggested that discerning between the effect of these variables and spring temperature can be difficult when they are correlated. In our study area, snowfall is scarce and concentrated between December and March, which is outside the period of FCOY den exit; therefore, we can discard snowfall as one of the main variables affecting the variability of den exit dates.

Although we did not record microclimatic characteristics of den sites because of their inaccessibility, we consider it important to point out here that the microclimate at den sites may also play a role in how a bear responds to environmental conditions around a den (Pigeon et al. 2016b). Another factor that has not been taken into account in this study, but may play a role in determining the length of hibernation, is the age and/or body condition of females in dens (Robbins et al. 2012). It is reasonable to think that the physical condition of a female might affect the reserves that the female has to spend during the hibernation period and to feed cubs, which in turn may influence the date of den exit.

In view of the relationship between den exit dates and spring temperatures, it is essential to consider the consequences that an increase in temperature in the current context of global change would have on the reproductive success and cub survival after den exit of brown bear populations, as already reported for winter temperatures (Albrecht et al. 2017). Predicted variations in air temperatures generally point toward an increase in temperatures (IPCC 2013), with projected increases of 2.0° to 4.9°C in global average temperature by 2100 (IPCC 2013; Raftery et al. 2017). In southwestern Europe, where our study population is located, increases in average temperature have already been observed in recent decades (Rodríguez et al. 2007; Penteriani et al. 2019). This general increase in temperatures would be especially noticeable in higher average temperatures in winter and spring (IPCC 2013). The changes in climate due to global warming, in particular those produced in colder periods, such as changes in winter–early spring temperatures and snow cover, can alter the phenology of many organisms (Williams et al. 2015). For example, these types of changes can cause mismatches between the biological cycle of animal species and the trophic resources on which they depend. In fact, this phenomenon has been described in other species (e.g., greater snow goose [*Chen caerulescens atlantica,* Doiron et al. 2015] and caribou [*Rangifer tarandus,* Post and Forchhammer 2008]). More specifically for hibernating mammals, lower fitness and reproductive success have been reported as a consequence of climate change (Lane et al. 2012; Turbill and Prior 2016), and specific episodes of variation in the end of hibernation in consecutive years with very different spring temperatures have been described (e.g., Mcloughlin et al. 2002). Advancement in den exit date and a shortening of the hibernation period in brown bears would therefore be expected. Particularly, brown bear populations in the mountains of southern Europe, such as the Cantabrian Mountains, might be especially affected. Published studies suggest that

(1) the effect of climate change will be more pronounced in mountainous areas (Root et al. 2003; Penteriani et al. 2019); and (2) increases in extreme climatic events, as well as anomalies in temperature and variability in precipitation, have been predicted to occur in southernmost Europe (Giorgi et al. 2004; Castro et al. 2005; Pendergrass et al. 2017). Thus, an earlier den exit date may cause possible mismatches between the chronology of hibernation and food availability. Moreover, it has been suggested that a premature den exit could affect the fitness of cubs, which are smaller and thus would be more vulnerable to predation and infanticide (Bellemain et al. 2006; Pigeon et al. 2016b).

Thus, understanding how climatic change might affect future den chronology is essential to predicting how the species will respond to this new human-induced challenge. This will be particularly important in our study area, because (1) our population, which inhabits the southern limit of the European bear range, is small and isolated; and (2) the Cantabrian Mountains are expected to be more severely affected than other areas by climate change, the latter having greater effects in mountainous landscapes (Root et al. 2003; Penteriani et al. 2019). Given the demonstrated influence of spring temperature on den exit, the predicted scenarios of climate change and the potential effects on brown bear populations, long-term studies on the chronology of hibernation and its relationships with external factors such as climate seem crucial for brown bear conservation.

Finally, although most reproductive dens in the Cantabrian Mountains are natural cavities in steep slopes or rocky cliffs, and thus far from humans and their activities (Penteriani et al. 2020b), we consider it important to highlight here that, when monitoring the chronology of bear hibernation, it is also necessary to take into account the possible interference of human activities (Evans et al. 2012). However, human-mediated den abandonment has prevalently occurred in areas with mild or moderate relief roughness and where dens are generally excavated in the ground or accessible from ground level (Swenson et al. 1997; Evans et al. 2012).

# *Chapter III*

# Rubbing behaviour of European brown bears: factors affecting rub tree selectivity and density

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## SUMMARY

Scent-mediated communication is considered the principal communication channel in many mammal species. Compared with visual and vocal communication, odours persist for a longer time, enabling individuals to interact without being in the same place at the same time. The brown bear (*Ursus arctos*), like other mammals, carried out chemical communication, for example by means of scents deposited on marking (or rub) trees. In this study, we assessed rub tree selectivity of the brown bear in the predominantly deciduous forests of the Cantabrian Mountains (NW Spain). We first compared the characteristics of 101 brown bear rub trees with 263 control trees. We then analysed the potential factors affecting the density of rub trees along 35 survey routes along footpaths. We hypothesized that: (1) bears would select particular trees, or tree species, with characteristics that make them more conspicuous; and (2) that bears would select trees located in areas with the highest presence of conspecifics, depending on the population density or the position of the trees within the species' range. We used linear models and Generalized Additive Models to test these hypotheses. Our results showed that brown bears generally selected more conspicuous trees with a preference for birches (*Betula* spp.). This choice may facilitate the marking and/or detection of chemical signals and, therefore, the effectiveness of intraspecific communication. Conversely, the abundance of rub trees along footpaths did not seem to depend on the density of bear observations or their relative position within the population centre or its border. Our results suggest that Cantabrian brown bears select trees based on their individual characteristics and their location, with no influence of characteristics of the bear population itself. Our findings can be used to locate target trees that could help in population monitoring.

## INTRODUCTION

Chemical signals that are spread by distinct means, such as urine, faeces, or glandular secretions (Müller-Schwarze 2006; Johnston and Del Barco-Trillo 2010), are considered the principal channel of communication in many mammal species (Ralls 1971), more so than visual or acoustic signals (Müller-Schwarze 2006; Penteriani and Delgado 2017). Mammalian scent-marking strategies mostly depend on individual and social factors, as well as on the physical characteristics of the environment (Barja and De Miguel 2010). Scent-mediated communication has several advantages, including persistence for long periods, and facilitation of interactions among individuals without any need for direct interaction at a given site (Mills et al. 1980).

Chemical communication can have different functions that include: self-advertising, i.e., communication of the state or characteristics of the individual, such as age, sex, reproductive status, and health condition; conspecific localisation; communication of dominance; and the defence of a resource (Brown 1979; Doty 1986; Gosling 1990; Johnston 2008; Morales-González et al. 2019). Sometimes, this form of indirect interaction also can prevent agonistic encounters (Gosling and McKay 1990; Roberts and Gosling 2001). While scent-marking plays an important role when defending or signalling territory occupancy in territorial species (Roberts and Gosling 2001; Müller and Manser 2008; Barja and De Miguel 2010), scent marking in non-territorial species is more difficult to interpret (Clapham et al. 2012). Solitary species must maintain effective communication to sustain a social structure that facilitates reproduction (Clapperton 1989; Gosling and Roberts 2001), for example by communicating male fitness (White et al. 2002) or the reproductive status of females (Gorman and Trowbridge 1989; Rich and Hurst 1998; Barja and De Miguel 2010). In particular, large-bodied solitary carnivorous species with large home ranges base much of their communication on olfactory chemical signals (Macdonald 1980; Gorman and Trowbridge 1989; Lamb et al. 2017a), which usually are left on conspicuous and permanent substrates, such as rocks and tree trunks (Kleiman 1966; Barja 2009; Allen et al. 2017). Thus, intensive marking behaviour on those substrates increases detectability and information transmission, reducing the investment of resources in communication (Alberts 1992; Gosling and Roberts 2001).

As in other solitary and non-territorial carnivores (Smith et al. 1989; Barja 2009), bears perform scent-marking on different substrates (Filipczyková et al. 2016). Indeed, rubbing behaviour has been documented in most ursid species, i.e., American black bear *Ursus americanus* (Burst and Pelton 1983; Sawaya et al. 2012) and Asiatic black bear *Ursus thibetanus* (Bromley 1965), giant panda *Ailuropoda melanoleuca* (White et al. 2002; Swaisgood et al. 2004; Nie et al. 2012), sloth bear *Melursus ursinus* (Laurie and Seidensticker 1977), Andean bear *Tremarctos ornatus* (Filipczyková et al. 2016; Kleiner et al. 2018) and brown bear *Ursus arctos* (Krott 1962; Shaffer 1971).

Brown bears exhibit a set of marking behaviours, including: urination; biting, scratching, and stripping bark; rubbing the back, shoulders, and head (Green and Mattson 2003; Puchkovskiy 2009; Clapham et al. 2012), and pedal and scent-marking at the base of trees and the surrounding area (Clapham et al. 2012; Sergiel et al. 2017). Marking, or rub trees (hereafter, RTs) have a key function in intraspecific communication in brown bears (Green and Mattson 2003; Clapham et al. 2012, 2013; Sato et al. 2014; Tattoni et al. 2015; Lamb et al. 2017a). Indeed, some studies have reported larger odoriferous glands and higher amounts of glandular secretion produced in individuals that show more pronounced rubbing behaviour (Tomiyasu et al. 2017). Other studies even have reported a different composition of glandular secretions between males and females (Rosell et al. 2011; Sergiel et al. 2017; Tomiyasu et al. 2017), which may facilitate identification of sex among bears (Jojola et al. 2012). In addition, the function of tree rubbing has been described as density-dependent, prioritizing the communication of dominance in situations of a high density of individuals (Lamb et al. 2017a). There are two main functions and advantages of chemical scents on RTs: (a) communication of dominance or fitness in adult males (Clapham et al. 2012; Tattoni et al. 2015; Lamb et al. 2017a) and related adult male avoidance by subadults (Jojola et al. 2012; Tomiyasu et al. 2017); and, (b) increasing the probability of finding a potential mate (Green and Mattson 2003; Clapham et al. 2012, 2014; Lamb et al. 2017a).

The pool of RTs in a given area provides a communication network through which individuals exchange information; this pool can be used over time for generations (Green and Mattson 2003; Clapham et al. 2013; Morgan Henderson et al. 2015). RTs commonly are located in the proximity of foot trails or unpaved roads that facilitate the transit of bears (Lloyd 1979; Green and Mattson 2003; Sato et al. 2014), with trail-oriented rubbing marks (Green and Mattson 2003), or at forest edges (Green and Mattson 2003; Puchkovskiy 2009). Brown bears seem to select trees that allow for greater conspicuousness of their markings. Preference also is given to certain species of conifers (Puchkovskiy 2009; Sato et al. 2014), probably due to the resins that may enhance the detectability or range of scent-markings (Green and Mattson 2003; Clapham et al. 2013; Tattoni et al. 2015). This effect has been suggested to be enhanced by producing wounds to the tree that increase resin flow (Sato et al. 2014).

Studies on RTs have mainly been focused on North American grizzlies *Ursus arctos horribilis* (Green and Mattson 2003; Clapham et al. 2013; Morgan Henderson et al. 2015), with a few also in Russia (Puchkovskiy 2009; Puchkovskiy et al. 2012) and Japan (Sato et al. 2014); however, these studies considered large continuous populations. To our knowledge, such a study has not previously been carried out in smaller, vulnerable populations, nor in populations living in areas dominated by deciduous forest. Here, by using (a) 101 RTs found in the Cantabrian Mountains (north-western Spain) and (b) the density of RTs along 35 survey routes along footpaths, we carried out a multilevel analysis to elucidate whether brown bears' RT selection is determined by tree species, physical traits, landscape position, and whether RT occurrence was related to their spatial location and observed bear density. Two main hypotheses underlie this study. First, as previously reported in populations inhabiting coniferous forests, RTs have characteristics that distinguish them from surrounding trees (e.g., dendrometric characteristics, tree location), which probably enhance the conspicuousness of chemical signalling and/or represent a better substrate for marking. We thus hypothesized that bears would select specific trees, or tree species with characteristics that make them more conspicuous. Second, we hypothesized that RTs would be more abundant in areas with the highest presence of conspecifics, towards the core of the bear distribution area and in areas where the density of bears is higher.

This study was carried out in a small and isolated, but still autochthonous, brown bear population, at the southwestern limit of the current species distribution. An overarching goal of the study therefore was to obtain information on scent-marking in small populations, whose behaviour may differ from larger and less isolated populations, because the smaller population size is likely to mean a higher number of interactions between the same individuals. The results provide insights into the ecology of a threatened population and therefore contribute to conservation and monitoring actions.

# METHODS

## Study area

The study area covers most of the geographic range of the western sub-population of brown bears in the Cantabrian Mountains (northwestern Spain, Figure 1), which run for ~300 km in parallel to the coast (E–W) with an average and maximum altitude of 1100 and 2648 m a.s.l, respectively (Martínez Cano et al. 2016; Penteriani et al. 2019). The region has an oceanic climate, more humid and temperate in northern slopes and continental and dryer on southern slopes (Ortega and Morales 2015). The landscape is covered predominantly by forests, shrubs, and croplands (Mateo-Sánchez et al. 2016). Forests of semi-deciduous and evergreen oaks (*Quercus* sp.) dominate sunny slopes, whereas the north-facing slopes are covered by deciduous trees such as beech (*Fagus sylvatica*) and common (*Q. robur*) and sessile oak (*Q. petraea*). Birches (*Betula* sp.) occupy areas of acid soils, dominant towards the west of the study area, in well illuminated areas with sufficient humidity and frequently colonizing degraded or bare areas, with few monospecific stands (García de Celis et al. 2004). Non-forested areas are mainly occupied by shrub species, such as heather (*Erica* sp., *Calluna* sp.) and brooms (*Cytisus* sp.; Fernández-Gil et al. 2006; Mateo-Sánchez et al. 2016). Above the treeline, berry-producing shrubs occur, including bilberries (*Vaccinium myrtillus*; Pato and Obeso 2012; Martínez Cano et al. 2016). Most of the areas inhabited by bears are surrounded by urbanized and cultivated areas, with a high density of transport infrastructure; the main economic activities include livestock breeding, mining, timber harvesting, and recreational activities (Zarzo-Arias et al. 2018, 2019).

## Description of the population

In northern Spain, there are two brown bear populations that are isolated from other European populations, one in the Pyrenees and another in the Cantabrian Mountains, separated from each other by almost 300 km. The latter population is divided into two subpopulations, with little gene flow (Pérez et al. 2010; Gonzalez et al. 2016) and a genetic variability that is among the lowest of any brown bear population in the world (García-Garitagoitia et al. 2007). In the 1990s, the Cantabrian population consisted of a minimum of 70 – 85 bears (50 – 65 individuals in the western nucleus and 14 – 20 in the eastern; Clevenger and Purroy 1991; Naves and Palomero 1993; Pérez et al. 2014). Recent population trends seem positive, especially in the western subpopulation (Pérez et al. [2014] reported 168 – 260 bears in the western subpopulation and 12 – 40 in the eastern subpopulation), but this species is still considered as "Endangered" in Spain (BOE 2011).

## Multilevel analysis

### Location and characterisation of rub and control trees

We surveyed principal trails and forest roads (hereafter footpaths) within the study area for RTs from October 2018 to March 2019 (Figure 1). We looked for trees with rubbing signs such as smoothed bark, discoloured surface, scratches, bites, or lack of vegetation at the base; however, the tree was only considered an RT when the presence of bear fur snagged on the bark was confirmed (a characteristic sign of bear tree rubbing behaviour). All the trees located within a radius of 5 m around each marked tree (following Clapham et al. 2013) were considered control trees (hereafter, CT). None of the CTs were found to have any evidence of marking. This radius ensured that we sampled trees that showed the same local habitat characteristics as the RT, and that were clearly available to the bear in that location. We followed previous studies on brown bear tree rubbing behaviour (Green and Mattson 2003; Clapham et al. 2013; Sato et al. 2014), to characterise each rub and control tree, recording the following variables: (1) tree species (categorical with five levels: birch [*Betula spp.*], oak [*Quercus* spp.], chestnut [*Castanea sativa*], conifer [*Pinus* spp., *Pseudotsuga menziesii*], and other); (2) tree status (categorical with two levels: dead and alive); (3) other brown bear tree marks (categorical with three levels: bites, scratches, no other marks); (4) slope exposure, i.e., exposure where the tree was located (categorical with eight levels: north, northeast, east, southeast, south, southwest, west, northwest); (5) tree height, measured with NASA GLOBE Observer v 3.0 (NASA 2019); (6) trunk height, i.e., from the ground to the first branch, measured with a tape measure; (7) diameter at breast height (DBH), measured with a diameter tape; (8) distance to the nearest footpath (hereafter dist. to footpath), measured with a tape measure; (9) tree spacing, i.e., average distance to the nearest tree located in each of the four main cardinal directions, measured with a tape; and (10) terrain elevation (m.a.s.l.).

All spatial analyses were carried out using QGIS software. All the layers used were extracted from transportation network information from CNIG (http://centrodedescargas.cnig.es/). We reclassified the existing land cover classes in the land use layer (IGN; Cartografía Temática Ambiental of the Principado de Asturias, Hojas del Mapa de Vegetación, Litología, Roquedos y Hábitat del Oso. Escala 1:25000. © Principado de Asturias, Spain) into six habitat types: (1) deciduous forests; (2) conifer forests; (3) shrublands; (4) pastures; (5) rocky areas; and (6) crops.

### Characterization of the study footpaths

To analyse variability in the abundance of RTs along footpaths, we estimated the following variables for each footpath: 1) rub tree abundance, i.e., the kilometric abundance index of rub trees for each footpath (the ratio of the total number of RTs observed along a footpath with respect to the total footpath length covered at each site; hereafter, RT abundance on footpaths); (2) predominant RT species (categorical variable with 6 levels: birch, conifer, chestnut, oak, mixed, and other).

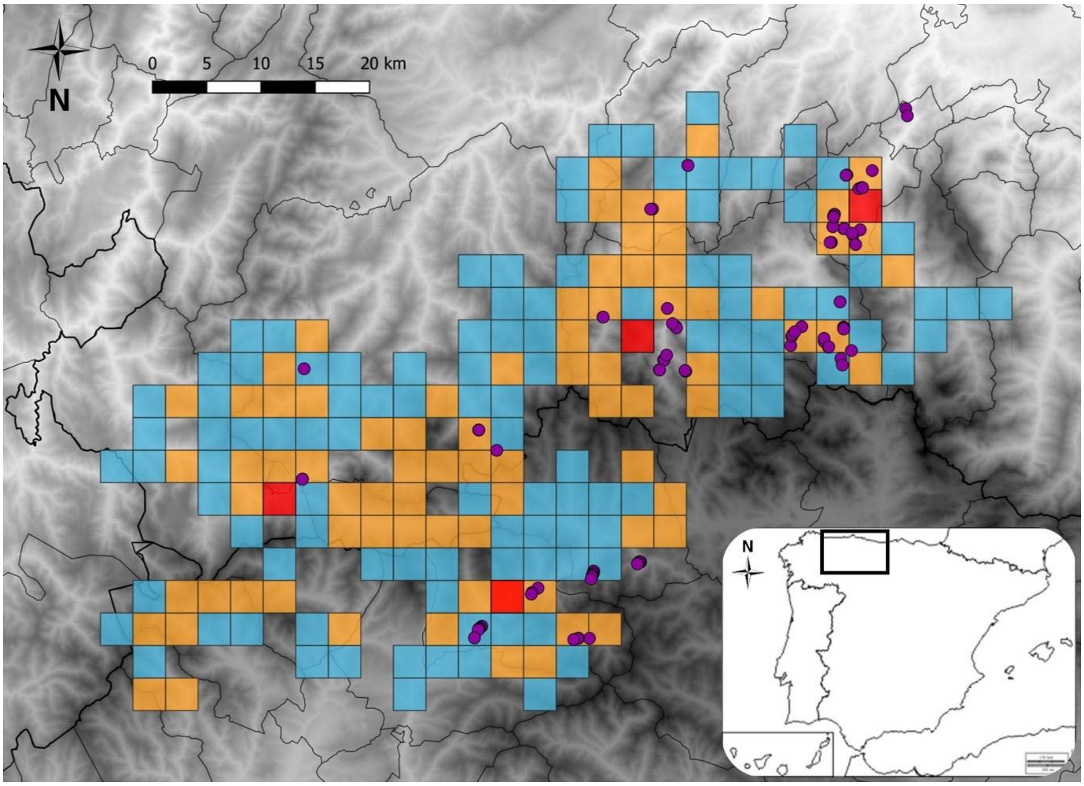


**Figure 1**. Locations of the RTs included in the study and the range of the western subpopulation of Cantabrian brown bear, divided into cells of different observation frequency. Inset shows location of mapped area within the geographic confines of Spain. Locations of the 101 brown bear rub trees located in the Cantabrian Mountains (NW Spain; provinces of Asturias and León) are represented with purple dots. Due to the short distance that separates rub trees in some cases, several trees can be under the same spot. The range of the western subpopulation of Cantabrian brown bear was calculated as 3x3 km cells with at least three continuous years of bear observations (since 2000; Lamamy et al. 2019a). The cells with only three continuous years of bear observations are in blue and were considered as the 'border cells'. The core areas, i.e., areas with at least seven years of bear presence, are in orange. Within the core areas, we calculated the 'core cells' (in red), i.e., cells within each of the core areas that showed the highest number of continuous years of bear presence.

Footpaths (length range 0.5 - 10.0 km) with at least 60% of RTs belonging to the same species were classified as paths characterized by that species, while footpaths without a predominant species were classified as ‘mixed’; (3) density of bear observations (see below) in a ring buffer of 1 km around each footpath where the RTs were found (hereafter, surrounding bear obs. density) as a proxy for the bear density around the RTs; and (4) the ratio of the distance to the nearest core cell with respect to the distance to the nearest border cell (ratio core/border). This last variable was a proxy for the relative position of the footpath in the area occupied by each population nucleus.

### Explanatory variables for RT abundance

We divided the area known to be inhabited by the western subpopulation of brown bears in the Cantabrian Mountains into cells of 3 × 3 km that were classified into: 1) border cells, i.e., cells with at least 3 years of confirmed bear presence; 2) core area cells, i.e., cells with at least 7 years of confirmed bear presence; 3) core cells, i.e., cells within each core area that showed the highest number of years of confirmed bear presence. Cells not included in any of these categories were not considered to be inside the brown bear range and therefore were discarded (Zarzo-Arias et al. 2019); Figure1). By undergoing this process, we obtained four different ‘core areas’ of bear distribution, i.e., cells with > 7 years of bear observations (Figure 1), whereas the border of this distribution represented our border of the bear population. For each of these core areas, we selected one ‘core cell’, i.e., the cell with the most years of bear observations for each core area (Figure 1). We calculated the distance from the central point of each footpath to: 1) the centroid of the nearest core cell (i.e., distance to core cell); and 2) the centroid of the nearest border cell (i.e., distance to border cell). We undertook this procedure in QGIS.

Brown bear observations used to obtain the values of the variables (i.e., surrounding density of bear observations, distance to core cell, and distance to border cell variables) were obtained for the period 2000 - 2017 by: (1) direct and indirect observations (scats, hairs and footprints) that were georeferenced by rangers of Principado de Asturias and Junta de Castilla y León, mainly by the 'Patrulla Oso' (Bear Patrol), as well as by all the other rangers of both regional governments, by the Asturian Foundation for the Conservation of Wildlife (FAPAS, Fondo para la Protección de los Animales Salvajes), by the Asturian Bear Foundation (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 the Bear Patrol; and (3) our own georeferenced observations (Sergiel et al. 2017; Lamamy et al. 2019; Penteriani et al. 2020b).

## Statistical analyses

In analysing the effect of individual tree characteristics on the probability of brown bear marking, it was necessary to account for the non-independence of rub and control trees sampled at the same location. We addressed this by adopting an approach that explicitly accounted for spatial autocorrelation using generalized additive models (GAMs; Hastie and Tibshirani 1986). This approach fits smoothing functions to easting and northing coordinates that account for non-linear spatial phenomena (i.e. spatial autocorrelation) and thus for the likelihood that coordinates close together will be more similar than those further apart. Given that rub and control trees have the same coordinates at a given sampling location, this approach controls for non-independence of these observations, as well as accounting for spatial autocorrelation at larger scales. GAMs were fitted with tree type as the binomial response variable (0 = control tree; 1 = rub tree) and the interaction between X and Y coordinates of trees as a smooth function (Wood 2004). We used the thin plate regression spline method with $k = 20$. This level of $k$ was chosen through visual assessment of the residuals, to ensure sufficient smoothing while at the same time avoiding overfitting. To maintain relatively simple models for running the scenarios, and to minimise overfitting, smoothed terms were not used for the other continuous explanatory environmental variables (e.g. Gili et al. 2020). The following predictor variables were included in the models to be tested: tree species, tree height, trunk diameter, trunk height, tree spacing, and distance to footpath. All the variables were scaled, and there was no collinearity among explanatory variables (maximum value of Variance Inflation Factor, VIF = 2.7).

Next, we investigated whether RT abundance on footpaths (the kilometric abundance index) varied depending on local density of bear observations, location of the footpaths with respect to bear population distribution, and the predominant tree species around each footpath. Because RT abundance on footpaths was likely to vary between the two main portions of the bear population (i.e. Asturias and León), we first extracted the residuals of the linear model (LM) including the RT abundance on footpaths as the response variable and the geographic location (two-level variable: Asturias and León) as a predictor. These residuals thus included the variation derived from the location of each footpath (geographic location) in the final model. Because the residuals of the model did not follow a normal distribution, we carried out a logarithmic transformation of RT abundance on footpaths (Gelman and Hill 2006) to achieve normality. We then built LMs with these values as the response variable and the three above-mentioned parameters as explanatory variables.

We carried out all statistical analyses with the package "lme4" (Bates et al. 2015) and "mgcv" (Wood 2004) for GAMs in R v.3.5.2 statistical software (R

Foundation for Statistical Computing 2018). To build both model classes (i.e., GAMSs and LMs), we carried out the following procedure: to identify possible collinearity among predictor variables, we calculated variance inflation factors (VIF; Fox et al. 2007) for coefficients in the full model. Influence diagnostics were used to assess the presence of potential outliers and highly influential observations in our models, though none were found. We used model selection to test all combinations of the predictor variables (including the null model). Model selection was based on Akaike's information criterion (AIC; Akaike 1973) using the library "MuMIn" (Bartoń 2013) and models with a ΔAICc < 2 were considered as equally competitive. We then employed multi-model averaging on the models with ΔAICc < 2 to extract coefficients of each explanatory variable.

## RESULTS

### Location and characterisation of rub and control trees

During this study, we found 101 RT and used 263 CT (Figure 1), with a range of 0 to 9 CT per RT.  Only 3 of the RTs (<3%) and 8 of the CTs (3%) were dead. Rubbing marks such as scratches and bites were present in 81.2% and 80.2% of the RTs respectively. RTs were located at an average altitude of 895 m a.s.l. and were predominantly on north-facing slopes: 31.7% N ($n$ = 32), 17.8% E ($n$ = 18), 12.9% S ($n$ = 13), 9.9% NE ($n$ = 10), 9.9% NW ($n$ =10), 7.9% W ($n$ = 8), 5.0% SE ($n$ = 5) and SW ($n$ = 5). Birches were the most frequently marked single tree type (28.7%), followed by oaks (16.3%), conifers (11.6%), and chestnuts (10.1%). Birches and conifers were marked at a higher percentage than that in which they appeared in the total pool of trees studied (18.6% and 7.5% respectively), while the rest of tree classes were marked in a similar proportion to their abundance. The results of the models testing for the effect of individual tree characteristics on the probability of being marked suggested that, among the variables considered, trunk DBH, mean distance to neighbouring trees, and tree species, were the most important characters in explaining tree marking probability (Table 1 and Figure 2).

**Table 1**. Mean value, standard deviation (SD) and minimum (Min) and maximum (Max) values of each of the parameters used to characterise both rub and control trees.

| | ***Rub trees*** | | | | ***Control trees*** | | | |
|---|---|---|---|---|---|---|---|---|
| | ***Mean*** | ***SD*** | ***Min*** | ***Max*** | ***Mean*** | ***SD*** | ***Min*** | ***Max*** |
| *Trunk diameter (cm)* | 26.5 | 19.0 | 7 | 180 | 17.3 | 10.1 | 0.3 | 70 |
| *Tree height (m)* | 11.9 | 4. 5 | 2 | 25 | 9.9 | 4.6 | 2 | 26.2 |
| *Trunk height (m)* | 3.6 | 2.2 | 0.3 | 13 | 3.2 | 2.4 | 0 | 15 |
| *Tree spacing (m)* | 4.1 | 1.6 | 1.7 | 9.0 | 3. 1 | 1.2 | 0.2 | 6.9 |
| *Distance to footpath (m)* | 1.6 | 7.4 | 0 | 50 | 2.4 | 6.4 | 0 | 50 |

Indeed, the best ranked model showed this combination of explanatory variables (Table 2). Specifically, RTs had larger DBHs and were in less dense parts of the forest stand (i.e., they showed higher distances from the nearest trees) compared to CTs. In addition, birches were the most frequently marked trees by bears among all tree classes (Tables 2 and 3). The smoothed spatial term was not significant in the full model ($\chi^2_2 = 2.36$, $P = 0.31$), and no model including this term was in the best model set (ΔAIC between the best model containing the smoothed term and the top model = 2.35), suggesting limited influence of spatial effects between RTs and CTs.

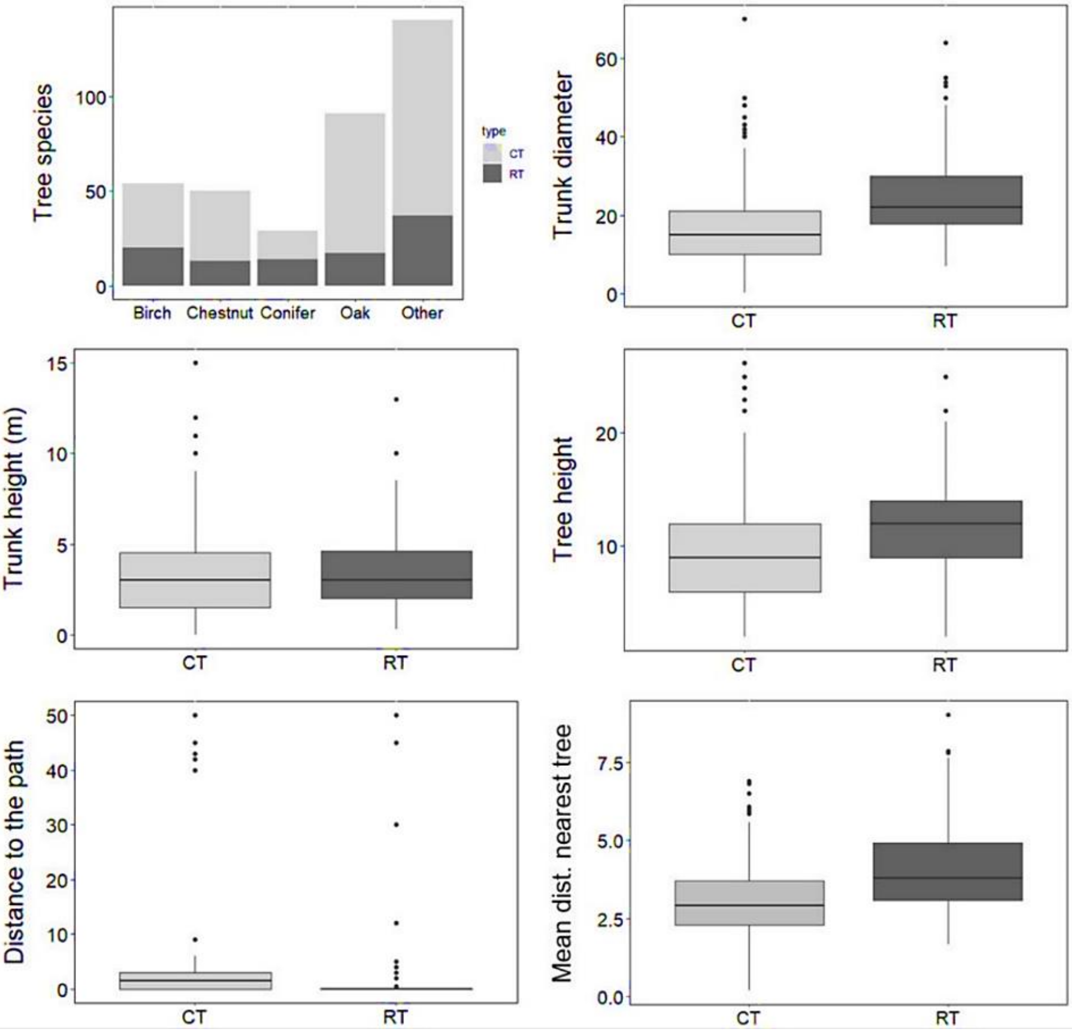


**Figure 2**. Characteristics of parameters used to describe rub trees (RT) used by brown bears ($n$ = 101 RT; dark grey) and control trees (CT; $n$ = 363; light grey) in the Cantabrian Mountains of NW Spain.

**Table 2.** Competing models from GAMs built to investigate individual tree characteristics (*n* = 364 trees) determining marking probability in the Cantabrian brown bear population. Competitive models are ranked from the lowest (best model) to the highest AICc value. Only models with ΔAICc < 2 are shown. Binomial response variable: tree type (0 = control tree (CT) and 1 = marked tree (RT)). R-squared of the most parsimonious model is 0.26. Note that a smoothed spatial coordinate term was included in the full model, but it was not selected in any of the top models.

| *Dependent variable* | *Competing models* | *df* | *AICc* | *ΔAICc* | *Weight* |
|---|---|---|---|---|---|
| **Tree type (CT/RT)** | **Trunk diameter + tree spacing + trunk height + tree species** | 8 | 368.58 | 0.00 | 0.23 |
| | Trunk diameter + tree spacing + tree height + trunk height + tree species | 9 | 368.91 | 0.32 | 0.20 |
| | Trunk diameter + tree spacing + tree species | 7 | 369.30 | 0.72 | 0.16 |
| | dist. to footpath + trunk diameter + tree spacing + tree height + trunk height + tree species | 10 | 369.36 | 0.78 | 0.16 |
| | dist. to footpath + trunk diameter + tree spacing + trunk height + tree species | 9 | 369.46 | 0.88 | 0.15 |
| | Distance to nearest footpath + trunk diameter + tree spacing + tree species | 8 | 370.18 | 1.60 | 0.10 |

**Table 3.** Effects of individual tree characteristics (*n* = 364 trees) on the probability that a given tree was a bear rubbing tree in the Cantabrian Mountains. For each explanatory variable, we report the estimate (β), standard error (SE), significance (p), confidence intervals (CI) and relative importance values (RIV) obtained from model averaging on the models with ΔAICc < 2. Binomial response variable: tree type (0 = control tree (CT) and 1 = marked tree (RT)). Baseline level for the categorical variable tree species is "other". The most important parameters are highlighted in bold.

| *Dependent variable* | *Explanatory variable* | *Model-averaged coefficients and relative importance values* | | | | |
|---|---|---|---|---|---|---|
| | | β | SE | p | CI | RIV |
| **Tree type (CT/RT)** | Intercept | -1.088 | 0.230 | $2.40^{e-06}$ | (-1.539; -0.637) | - |
| | **Trunk diameter** | **0.917** | **0.226** | **$5.14^{e-05}$** | **(0.474; 1.360)** | **1.00** |
| | **Tree spacing** | **0.698** | **0.143** | **$1.10^{e-06}$** | **(0.419; 0.979)** | **1.00** |
| | **Trunk height** | **0.275** | **0.152** | **0.072** | **(-0.023; 0.573)** | **0.73** |
| | **Birch** | **0.834** | **0.385** | **0.031** | **(0.079; 1.589)** | **1.00** |
| | Chestnut | -0.363 | 0.447 | 0.418 | (-1.239; 0.513) | 1.00 |
| | Conifer | 0.055 | 0.602 | 0.928 | (-1.125; 1.235) | 1.00 |
| | Oak | -0.558 | 0.383 | 0.146 | (-1.309; 0.193) | 1.00 |
| | Tree height | -0.301 | 0.217 | 0.168 | (-0.726; 0.124) | 0.35 |
| | Dist. to footpath | -0.181 | 0.167 | 0.279 | (-0.508; 0.093) | 0.41 |

## Characterization of the landscape around rub trees

The landscape surrounding the RTs was covered predominantly by deciduous forest, followed by scrubland and pastures, without any human settlements within a 1 km radius (Table 4).

**Table 4**. Mean value, standard deviation (SD) and range of landscape features surrounding rub trees, including the- percent of the different land cover within a 1km buffer around each rub tree.

| ***Parameters*** | ***Mean ± SD*** | ***Max - Min*** |
|---|---|---|
| *% Deciduous forest* | 62.1 ± 21.6 | 97.3 - 22.1 |
| *% Conifer forest* | 0.93± 4.1 | 23.6 – 0.0 |
| *% Shrubland* | 16.7 ± 15.6 | 56.2 – 0.0 |
| *% Pasture* | 7.7 ± 8.8 | 37.9 – 0.0 |
| *% Crops* | 2.4 ± 5.4 | 31.0 – 0.0 |
| *% Rocky areas* | 5.9 ± 12.1 | 46.8 – 0.0 |
| *Ruggedness* | 18435.9 ± 2965.6 | 25841.3 - 13436.5 |
| *Distance to the nearest paved road (m)* | 927.1 ± 1008.4 | 5617.7 - 12.4 |
| *Distance to the nearest unpaved road (m)* | 1267.2 ± 672.1 | 2948.1 - 156.0 |
| *Distance to the nearest river (m)* | 298.1 ± 282.1 | 1310.1 - 1.1 |
| *Distance to the nearest human settlement(m)* | 10522.0 ± 4929.6 | 18768.7 - 2781.9 |
| *Total length of paved roads (m) (1km buffer)* | 1489.47 ± 1409.87 | 6118.82 - 0.00 |
| *Total length of unpaved roads (m) (1km buffer)* | 447.87 ± 855.04 | 3407.23 - 0.00 |
| *Total length of rivers (m) (1km buffer)* | 2442.65 ± 1098.83 | 4849.03 - 0.00 |

## Characterization of the study footpaths

To assess the kilometric abundance of RTs, we included 35 footpaths. These footpaths had 0 to 11 RTs, with an average of 3.7 RTs per footpath (*SD* = 2.6, *n* = 35). The mean RT abundance on footpaths was 2.5 RTs/km (*SD* = 2.1, *n* = 35). The footpaths located in areas with a predominance of birch showed on average a higher density of RTs (3.3 ± 3.5 RTs/km, *n* = 9) compared to footpaths dominated by conifers (2.4 ± 1.5 RTs/km, *n* = 5), chestnut trees (1.9 ± 0.4 RTs/km, *n* = 3), oaks 1.9 ± 0.9 RTs/km, *n* = 4), other species (3.0 ± 3.4 RTs/km, *n* = 3), and those without dominant species (mixed; 2.0 ±

0.7 RTs/km, $n$ = 11). Along the footpaths, we detected some notably dense clusters of RTs, particularly in some footpaths located in birch forests (7 and 11 RTs in sections of 460 m and 930 m, respectively). In one case, we found a cluster of RTs in a homogeneous beech forest, with 7 RTs within 210 m of each other.

The set of models built to analyse potential factors affecting the intensity of bear rubbing, measured as the number of RTs along a footpath, showed that none of the variables under study played an important role. Indeed, the model with the lowest AICc value was the null model (Table 5). The second ranked model showed a weak positive relationship between RT abundance on footpaths and bear observation density (Table 5 and Figure 3); however, the importance of this variable was very low (Table 6).

**Table 5.** Competing models built to investigate the effect of ecological characteristics of the surroundings of the study footpaths ($n$ = 35) on the abundance of brown bear rub trees. Competitive linear models are ranked from the lowest (best model) to the highest AICc value. Only models with ΔAICc < 2 are shown. R-squared of the model including bear obs. density = 0.062.

| *Dependent variable* | *Competing models* | *df* | *AICc* | *ΔAICc* | *Weight* |
|---|---|---|---|---|---|
| RT abundance on footpath residuals | Null model | 2 | 66.50 | 0.00 | 0.52 |
| | Surrounding bear obs. density | 3 | 66.66 | 0.16 | 0.48 |

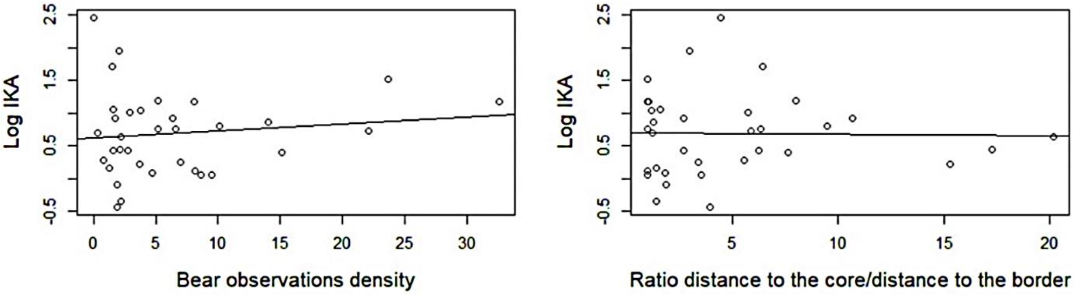


**Figure 3**. Changes of the logarithm of the RT abundance on footpaths of brown bear rub trees (LogIKA) along footpaths in the Cantabrian Mountains with respect to a proxy of brown bear density (left panel) and the position of the trail (right panel) within the bear population's range (see also Figure 2). Details on the proxy of bear density and the ratio core/border distance are provided in the main text.

**Table 6.** Effects of ecological characteristics of the surroundings of the footpaths (*n* = 35) located in the Cantabrian Mountains on the abundance of brown bear rub trees. For each explanatory variable, we report the estimate (*β*), standard error (*SE*), significance (*p*), confidence intervals (*CI*), and relative importance values (*RIV*) obtained from model averaging on the models with ΔAICc < 2.

| ***Dependent variable*** | ***Explanatory variable*** | ***Model-averaged coefficients and relative importance values*** | | | | |
|---|---|---|---|---|---|---|
| | | ***β*** | ***SE*** | ***p*** | ***CI*** | ***RIV*** |
| RT abundance on footpath residuals | Intercept | $3.354^{e-18}$ | $9.998^{e-02}$ | 1.000 | (-0.196; 0.196) | - |
| | Bear obs. density | $1.485^{e-01}$ | $1.005^{e-01}$ | 0.155 | (-0.048; 0.345) | 0.48 |

## DISCUSSION

In this study, we assessed brown bear selectivity of rub trees and the potential factors associated with marking behaviour along forest paths. It seems that Cantabrian brown bears select larger and more accessible trees, and that RT abundance is not determined by the density of bear observations or their geographical position within the bears' population range.

Specifically, brown bears preferentially used trees with greater trunk diameter. A preference for larger diameter trees also has been reported in studies spread throughout the brown bear range in North America (Green and Mattson 2003; Clapham et al. 2013), Russia (Puchkovskiy et al. 2012; Seryodkin 2014) and Japan (Sato et al. 2014). Trees with larger diameters may stand out over the surroundings and thus be more conspicuous (Green and Mattson 2003), which may also help if chemical signalling is associated with visual marks such as bites and scratches (Sato et al. 2014). This enhancement related to conspicuousness could be expected if the act of marking trees produces scent, as occurs when the bark is altered or when the marks are produced by pedal marking (Sergiel et al. 2017). Trunk height was almost significant, despite appearing in the best models, which probably suggests a trend towards greater height between the ground and the first branches in the selected trees. Greater trunk heights (i.e., the available vertical space in which the bears can rub) have also been observed for rub trees in North America (Green and Mattson 2003; Clapham et al. 2013) and Russia (Seryodkin 2014), and might result in greater accessibility for signallers and facilitate the action of rubbing (Seryodkin 2014), particularly for the largest bears. Rub trees were predominantly located on north-facing slopes, as also reported by Seryodkin (2014). Tattoni et al. (2015), in a study with camera traps, detected a higher cumulative camera trapping rate in NE and S aspects, orientations that in this study represented the 3rd and 4th position. Because most of the tree species included in this study develop better in the wetter conditions of northern slopes, e.g., beeches (Sánchez et al. 2003), chestnuts (Blanco Andray et al. 2000), sessile oaks (Díaz-Maroto et al. 2006), and birches (García et al. 2005), it seems plausible that the greater abundance of brown bear RTs is related not to the exposure itself, but to the fact that on these northern slopes forest stands are better developed and the trees grow larger than on the southern slopes.

Although our RT surveys were carried out exclusively along footpaths, we highlight here that in most studies on bear marking, trees were predominantly located along routes, game trails, and forest edges. Indeed, increasing distance to the footpath represented an explanatory, negatively-related variable with the probability of rubbing in other studies (86% in Green and Mattson 2003 and 100% in Clapham et al. 2013). Similarly, higher intensity of usage of RTs on large trails and forestry roads have been described in the Italian Alps, probably because they are preferred movement routes by bears (Tattoni et al. 2015). Some authors argue that observations of rubbing hairs, bites and scratches oriented towards roads and footpaths represent strong evidence that bears prefer to perform chemical signalling specifically on those trees located on the sides of footpaths and trails (Lloyd 1979; Burst and Pelton 1983; Green and Mattson 2003; Nie et al. 2012), which also are routes of brown bear displacement (Burst and Pelton 1983; Seryodkin 2014).

Even though we did not carry out an extensive census of all the tree species within the marking tree stand, we established whether the RT species were similar to those in their surroundings by comparing the RTs with their surrounding CTs. Thus, we discovered that birch was the tree species most frequently marked by brown bears, because it was found in greater proportion among marked trees than among all trees. Conifers also were marked in a greater proportion to their availability. However, the conifer species marked by bears in our study (Monterey pine [*Pinus radiata*] and Douglas fir [*Pseudotsuga menziesii*]) do not occur naturally in the study area, and the individuals included corresponded to plantations or groups of feral trees. Conifers are frequently identified as preferred rub trees because of the aromas they produce when they are lacerated (Puchkovskiy 2009; Nie et al. 2012; Clapham et al. 2013; Sato et al. 2014), which can enhance or help maintain the bear's scent and/or attract recipient bears. However, our study area did not have enough locations where coniferous and deciduous species co-occur to test for a potential preference for conifer rubbing by Cantabrian brown bears.

In our study area, birch is distributed irregularly, generally in acidic and wet soils or near water at forest boundaries or in cleared areas, forming continuous forests only in a few areas at high elevation (García de Celis et al. 2004). Nevertheless, it was proportionally the most marked tree species. For instance, in those places where several birches occurred along a path, most of them were marked, sometimes every few meters. Similar findings have been reported by studies conducted in boreal conifer-dominated forests, where birches were found to be marked more frequently than other deciduous species. For example, Puchkovskiy (2009) reported that in several forests of the Russian taiga, birch was the most frequently marked deciduous tree and that when birches were present, brown bears always chose it preferentially over other deciduous species. In addition, Seryodkin (2014) described the appearance of brown bear marking trees in Kamchatka forests dominated by the stone birch *Betula ermanii*. Preference for birch species also was reported in the Middle Sikhote-Alin, SE Russia (Seryodkin et al. 2014), suggesting that brown bears selected birch not only for their availability, but also for physiognomic characteristics that favour marking. In fact, birches tend to have a large diameter with no branches on the first few metres of the trunk, and the stratified bark is lacerated easily by scratches and bites. Also, the birch has a whitish outer layer contrasting with a dark inner layer, so when it is removed or lacerated the marks are very evident, even after healing, which may increase the conspicuousness of brown bear visual markings. In addition, in the common case of a birch RT surrounded by other tree species, generally characterised by darker barks (*Quercus* spp., beech, chestnut, etc.), the RT itself would stand out in the surroundings, thus making its visual traceability easier for bears and therefore becoming an advantageous and long-lasting substrate for marking. Marking has been suggested to include visual and olfactory signalling in different bear species, including brown bears (e.g., Sergiel et al. 2017), and different types of marking behaviour have been documented in social and solitary carnivores (e.g., Paquet 2011; Vogt et al. 2014).

It is worth noting that the sections dominated by birches had the highest rubbing densities. RT densities in the Cantabrian Mountains are higher than those recorded by Henderson et al. (2015) in conifer forests of the northwest US, where they compared RT abundances between developed trails and roads (1.0 ± 1.1 RTs/km; $n$ = 30) and game trails (0.8 ± 1.1 RTs/km; $n$ = 30). In several Kamchatka valleys dominated by stone birch, Seryodkin (2014) reported very variable abundances (from 40 RTs / km to 0.4 RTs / km) and RTs groupings in short sections of the footpath (7

RTs in 20 m or 5 RTs in 8 m). We detected similar but lower density aggregations, especially in birch-dominated forests. This indicates a trend towards more intense or greater marking on them, supporting the positive selectivity towards birches described above. Understanding wildlife behaviour can prove useful for conservation and management (e.g., Greggor et al. 2019). In the context of our study, the noticeable selection of birch by marking bears might provide a tool to monitor bear presence, e.g., in areas immediately surrounding the present range of the species, where targeting birches in monitoring programs that search for bear signs might help detect dispersing individuals.

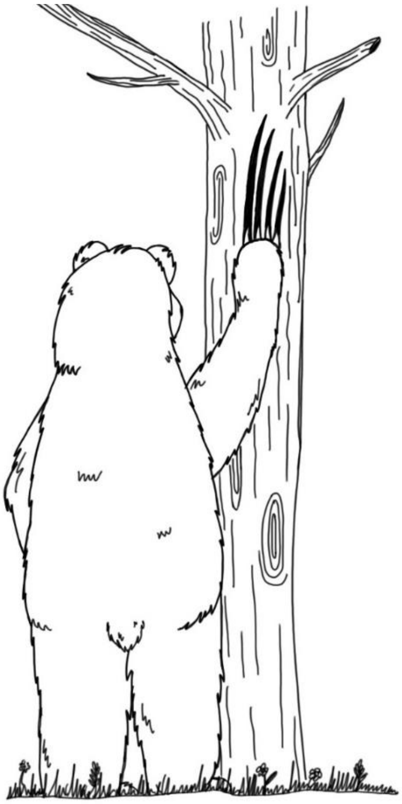
To our knowledge, this is the first time that the density of brown bear rub trees has been compared with some features of the bear population or its proxies. In our study, neither the density of bear observations (as a proxy for bear density), nor the position of the track within the bear distribution area, affected the kilometric abundance of RTs. Because the null model had the lowest AIC, we deduce that the determinants of the intensity of rubbing in our population are different from those analysed in this study, hence the assessment of other possible variables may be necessary. The lack of an effect of the density of observations on the density of rub trees may be due to the fact that differences in bear density, or more specifically of bear observations around each foot path, are not large enough to affect abundance from rub trees. More research in this field is needed to elucidate whether variations in bear density can affect rubbing behaviour in other ways, such as modifications in the frequency of rubbing or the proportion of rubbing between sex and age classes, as Lamb et al. suggested (2017). In one study considering the distribution of rubbing sites in a territorial carnivore, the tiger (*Panthera tigris*), rubbing increased towards the limits of the territory (Smith et al. 1989). This might not be applicable to brown bears that are non-territorial species in which individuals of the same population can have overlapping home ranges (Seryodkin et al. 2017; Frank et al. 2018).

There are three potential biases in this study. First, searches for RTs were undertaken mostly (but not exclusively) from footpaths. The findings that RTs were closer to, and orientated towards, footpaths may thus have been the result of greater detectability from those paths. However, we do not believe this to have affected our results given the large amount of evidence that footpaths are common routes of brown bear displacement and that RTs occur more frequently along such routes (e.g., Nie et al. 2012; Seryodkin 2014; see above). Second, the lighter coloured bark of birch trees may have made them more conspicuous to observers. We believe this potential bias was minimised by very careful observations of all potential RTs. Furthermore, preference for birch has been found in several other studies (see above). Third, we used proxy measures to estimate bear density and distribution. We cannot know whether our measures are fully accurate representations of the population but nevertheless, our measures were the best available, being based largely on observations made by trained forest rangers and researchers. While we believe the above potential biases were minimised in our study, their effects only can be properly elucidated through further research based on intensive telemetry studies.

To conclude, our results suggest that Cantabrian brown bears select rub trees based on characteristics related to the tree, rather than their position relative to areas with a high density of conspecifics and/or with the distribution of individuals within the population range. Thus, even in small and isolated bear populations, such as the one under study here, some aspects of rubbing behaviour such as tree selection and marking effort may not be affected by population size and/or structure.

# *Chapter IV*

# Visual marking in mammals first proved by manipulations of brown bear tree debarking



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***Scientific Reports*** **11, 1–6 (2021)**

## SUMMARY

The rather limited human ability to understand animal vision and visual signalling has frequently clouded our expectations concerning the visual abilities of other animals. But there are multiple reasons to suspect that visual signalling is more widely employed by animals than previously thought. Because visibility of visual marks depends on the background in which they are seen, species spending most of their time living in dark conditions (e.g., in forests and/or having crepuscular and nocturnal habits) may rely on bright signals to enhance visual display. Here, as a result of experimental manipulations, we present, for the first time ever, evidence supporting the use of a new channel of intraspecific communication by a mammal species, i.e., brown bear Ursus arctos adult males relying on visual marks during mating. Bear reactions to our manipulation suggest that visual signalling could represent a widely overlooked mechanism in mammal communication, which may be more broadly employed than was previously thought.

## INTRODUCTION

Among the many groups of terrestrial species, our understanding of mammal visual signalling might be hampered by the fact that most research on mammals has focused on chemical (e.g., scat, urine, and glands) and acoustic (e.g., howling) signalling. Instead, visual communication might be an overlooked communication channel (Caro et al. 2017; Penteriani and Delgado 2017), despite being perhaps as important as the others, if we consider that: (1) mammal colouration has evolved for inter- and intraspecific communication (Caro 2009; Caro et al. 2017; Penteriani and Delgado 2017; Moreira et al. 2019; Caro and Mallarino 2020), which means that mammals use visual signals to communicate; and (2) visual signalling through physical marks (e.g., bites and scratches) is permanent and, thus, has the obvious advantages of (a) being long-lasting, i.e., environmental factors such as rain or snow are less likely to affect the detectability of visual marks as compared to, e.g., chemical signalling (Burst and Pelton 1983), although mammals have found strategies to make chemical signalling last as long as possible (Mohorović and Krofel 2020), and (b) functioning remotely, i.e., even when the signaller is away from the marked location (Penteriani and Delgado 2017). Visual marking may also allow individuals to reduce repeated visits to strategic marking points, and thus save time and energy, which would otherwise detract animals from other activities, like foraging and reproduction (Gehring 2018). Therefore, visual signalling may represent a reliable and advantageous communication channel (Burst and Pelton 1983).

Solitary species like bears may benefit from advertising their location, size, and reproductive status to expedite mate selection during the breeding season. Moreover, brown bears usually occur at low densities across their range, making direct interactions with one another infrequent (Steyaert et al. 2012; Swenson et al. 2020).

Thus, long-lasting visual signalling may be particularly effective and considerably time saving. To date, studies on bear communication have highlighted two main forms of communication (Clapham et al. 2013, 2014; Lamb et al. 2017a; Sergiel et al. 2017; Gehring 2018; Revilla et al. 2021): (1) olfactory communication, i.e., the marking of focal trees by rubbing the body against the trunk and/or by urination and deposition of anogenital gland secretions; and (2) pedal marking, by which bears mark the ground with their scent by grinding their feet into the substrate. Auditory communication, e.g., vocalizations used as threats during agonistic encounters, to advertise sexual receptivity, or for communication between females and their cubs, is considered as the least important channel through which bears signal, whereas visual communication has always been considered limited to different forms of body postures or behavioural displays (but see Penteriani et al. 2020b). Since the beginning of the 1980s, bear marks on trees have puzzled researchers (Burst and Pelton 1983). The function of, and motivation behind, tree biting and clawing have prompted a variety of theories related to glandular scent deposition (i.e., chemical signalling), but none of these hypotheses has been considered satisfactory, nor have they ever been tested (Burst and Pelton 1983). The debarking behaviour of brown bears *Ursus arctos*, which leaves bright and conspicuous marks on tree trunks (see Supplementary Data Figure 1 and Supplementary Data Figure 2), presents a unique yet unexplored opportunity to investigate new ways of visual communication in terrestrial mammals, and to better understand both bear and carnivore communication broadly. The hypothesis behind this experimental work is that brown bears may rely on visual communication via the conspicuous marks that they produce on trees.

# METHODS

## Manipulation of trunk debarking

Twenty trees with brown bear marks on their trunks (González-Bernardo et al. 2021) were used for bark manipulations from the 1st of May 2020 (the beginning of the mating period in the Cantabrian Mountains, Martínez Cano et al. 2016) to the end of September 2020 (the beginning of the hyperphagia period in this area, Martínez Cano et al. 2016), when trunk marking is supposed to stop or, at least, to decrease, Burst and Pelton 1983b). Strips of bark of the same species as the marked trees were used to cover bear marks (Supplementary Data Figure 3). We collected strips from the ground or we debarked a distant (preferably recently died) tree to avoid any further interaction with the trees marked by bears. Control bark strips were used on: (a) the same trunks as the manipulated bear marks, (b) the nearest tree of the same species as the manipulated one, and (c) the nearest rubbing trees with no bear marks. Control strips were used to discard the possibility that brown bears were attracted by our scent and removed the strips for any reason other than to uncover their visual marks. Additionally, in four cases where a bear removed the mark manipulation, it was possible to cover the bear mark again to reinforce support for the importance of visual signalling in brown bears. All manipulated trees were checked approximately every 15 days.

In five of the manipulated trees camera, traps were deployed (Browning Dark Ops HDProX) from May to August 2020. This period has been considered the one in which debarking is most intense in bears, Burst and Pelton 1983b). Camera traps were programmed to record, when triggered by an animal, one-minute videos during the day, and 20-second videos at night, with a one-second trigger delay between videos. All sites were visited every two weeks to check if the bark manipulations had been removed and to service camera traps (e.g. battery check, eventually stolen cameras). Additionally, to document brown bear debarking behaviour away from of our manipulations, from January 2019 to July 2020 six additional camera traps were deployed to monitor six previously known rubbing trees highly frequented by bears, but where no visual marks were found (e.g., Supplementary Data Figure 4).

## Conspicuousness of brown bear visual marks

To explore the possibility that brown bear tree marking is a conspicuous signal on a trunk, we measured the contrast between the bark and sapwood for each of the marked tree species, as a proxy of mark brightness and conspicuousness. Using a blade, we first removed a small section of bark (approximately 3 x 4 cm, outer and inner bark) from three different trunks for each tree species. Bark removal exposed the sapwood, as happens in brown bear debarking. We took a total of 36 tree photos (JPEG format, 7 MG each), corresponding to 3 individuals from each of the 12 tree species where visual marking was detected: sycamore maple *Acer pseudoplatanus*, hazel *Corylus avellana*, birch *Betula pubescens*, chestnut *Castanea sativa*, cherry *Prunus avium*, ash *Fraxinus excelsior*, beech *Fagus sylvatica*, whitebeam *Sorbus aria*, Monterey pine *Pinus radiata*, oak *Quercus petraea*, willow *Salix caprea*, and linden *Tilia platyphyllos*. For repeatability purposes (Penteriani et al. 2006, 2020c), we took six measurements of bark brightness (three measurements of the bark and three of the exposed sapwood) for each picture. Finally, we calculated mean brightness values for both the cortex and the sapwood, and afterwards we calculated the contrast value (i.e., brightness of the bark - brightness of the sapwood) for each picture, for statistical purposes. Brightness values were obtained by processing the images with the Java-based image processing program ImageJ (https://imagej.nih.gov/ij/), by means of the Oval Selection Tool (width = 200 pixels, height = 200 pixels) and the Measure Tool.

Digital images are two-dimensional grids of pixel intensity values with the width and height of the image being defined by the number of pixels in x (rows) and y (columns) directions. Thus, pixels (picture elements) are the smallest single component of digital images, holding numeric values (pixel intensities) that range between black and white. RGB pixels are converted to brightness values using the formula = (red + green + blue)/3 (ImageJ User Guide IJ 1.46r, http://imagej.nih.gov/ij/docs/guide).

## Tree species selection for marking purposes

To study whether brown bears might select specific trees on which to leave visual marks because, e.g., of the conspicuousness of the mark and/or the ease of debarking, we used a set of 59 debarked trees previously recorded in the Cantabrian Mountains (González-Bernardo et al. 2021) to walk 59 linear transects with the aim of comparing the frequency of the tree species debarked by bears *vs*. the abundance of each tree species around the marked tree. Each transect had a total length of 40 m (20 m up and 20 m down from the marked tree), and the total number of trees of each species was recorded. The mean (± SD) number of trees (all species together) recorded was 13.0 ± 6.7 (range = 1 – 30 trees).

## Statistical analyses

We first compared the average brightness of bark with the average brightness of sapwood (n = 36 pictures) using a paired *t-test* ($\alpha = 0.05$). Second, to assess the variation in contrast among tree species, we built a linear model with contrast as the response variable, and species as the explanatory variable. Analyses were performed in R 3.5.1 statistical software (R Core Team 2018).

## RESULTS AND DISCUSSION

### Brown bear responses to marked tree manipulations

After concealing bear marks due to trunk debarking with bark strips from the same tree species (see Methods), our manipulations on 20 trees triggered a rapid reaction from brown bears. Between the 16th of May and the end of September 2020 (overlapping part of the brown bear mating period in the Cantabrian Mountains (Martínez Cano et al. 2016)), brown bears removed the strips of bark that we used to cover the trunk marks in 9 (45%) out of the 20 manipulated trunks (Figure 1 and Supplementary Data Figure 5). However, if we consider that these nine trees were also the ones that we could manipulate (because of field work restrictions due to COVID-19) from the start of the mating season (beginning of May), 100% of the bark strips used to cover tree marks were removed by bears when the manipulation occurred at the commencement of the mating season. In only one case, a bear removed the bark strips covering marks on a tree that was manipulated later in the mating season (end of June). Control bark strips fixed to (a) the same trunk as the manipulated bear mark, (b) the nearest neighbouring tree to the manipulated one showing bear marks, and (c) the nearest rubbing trees with no bear marks, were never removed by bears. In two cases (50%), after the first removal of the manipulated mark by a bear, which was subsequently covered again with new strips (n = 4), a bear removed the strips a second time. Further, camera traps showed that: (1) bears uncovered the manipulated marks the first time they visited the tree after our manipulation; (2) bark strips that were not removed were always the result of bears not visiting the site after tree manipulations; and (3) the shortest lapse of time between a mark manipulation and a bear visiting the tree for the first time and uncovering the mark was seven days. Thus, manipulations always triggered a rapid response from bears when adult males, probably the same individuals that debarked the trunks, came back and check on marked trees.

**Figure 1.** Brown bear response to trunk mark manipulation. The behavioural sequence of an adult male brown bear removing the pieces of bark that we used to conceal the visual markings on an ash tree during the mating season in the Cantabrian Mountains, Spain (12/06/2020, 15h37). The whole sequence is shown in the video footage Supplementary Data Figure 5.

## Conspicuousness of brown bear visual marks

The conspicuousness of a visual signal is not only increased by its position in a noticeable location, but also by the contrast between the signal and its background (Rosenthal and Ryan 2000; Bradbury and Vehrencamp 2011). A remarkable difference (pixel intensity: mean (± SD) = 85.09 ± 26.77, range = 20.27 – 177.06) exists between bark and sapwood brightness for all tree species ($t$ = 19.07, $p$ = $<2.2^{e-16}$) (Supplementary Data Figure 1). Even if contrast values for certain tree species, such as linden *Tilia platyphyllos* ($p$ = 0.05) and hazel *Corylus avellana* ($p$ = 0.09), were considerably higher than those for the rest of the species, the debarked tree species showed no remarkable differences in contrast among them ($F$ = 1.11, $p$ = 0.39, $R^2$ = 0.03), which suggests that a debarked tree is always conspicuous, independent of bark colour.

## Tree species selection for marking purposes

Debarked trees belonged to species relatively scarce in forest stands, i.e., only 31.1% ± 29.4 of the trees recorded in the proximity of a marked tree (see Tree species selection for marking purpose in Methods) were of the same species as the trees marked by bears. Moreover, in only 19 of the 59 covered transects (33.90%), the tree species marked by bears was the most abundant one. These percentages decrease if we remove a single monospecific forest stand of planted Monterey pine *Pinus radiata*. Indeed, if we only take into account native forest stands: (a) only 26.2% ± 26.2 (range = 0 – 85.7%) of the trees recorded in the proximity of the marked tree corresponded to the same species as the tree marked by a bear; and (b) in only 26.4% of transects, the tree species marked by bears was the most abundant one. This suggests that bears may select for some tree species, probably because of the characteristics of their bark, e.g., softness (Richter 2015).

## Visual marking function

After manipulating bear tree marks in the Cantabrian Mountains (north-western Spain), we found that bears removed the bark strips that we used to cover their marks during the mating season (Supplementary Data Figures 4 and 6), suggesting that bear debarking may represent a visual communication channel used for intraspecific communication.

Dominant males use chemical signalling to communicate and maintain dominance over other males and, consequently, subordinate males have been shown to scent-mark less than dominant males and in some cases not scent-mark at all (Clapham et al. 2013, 2014; Lamb et al. 2017a). Our two-year video recordings (Supplementary Data Figures 4, 6 and 7) show analogies between chemical and visual signalling, the latter being also mainly performed by adult males during the mating season.

Interestingly, clawing and biting the bark of a tree, often leaving fur, frayed bark and scars on the tree trunk or other substrates, have always been considered olfactory signals (Gehring 2018; Cornhill and Kerley 2020). For example, it has been suggested that clawing may leave scent from pedal glands and biting may deposit saliva (Gehring 2018). Yet, at least for brown bears, the amount of smell left by scratches and bite marks on trees is expected to be less than that left by secretions from sebaceous and apocrine glands when rubbing the whole body (Gehring 2018) and, thus, might result in an unnecessary reinforcement of body rubbing. Moreover, visual marks are generally on the upper sections of the tree, which can only be reached by larger adult males, and furthermore they would not be reached while body rubbing (Supplementary Data Figure 8). This may explain why adult males use multiple marking behaviours to leave two different signals, i.e., chemical and visual, which may complement each other (Burst and Pelton 1983). For example, whereas a chemical signal provides information on bear sex and individuality, visual marks might simultaneously indicate the height of the bear, thus providing a signal that is physically associated with a quality of interest to the receiver (Maynard Smith and Harper 1995). A similar behaviour has been suggested for tigers, *Panthera tigris*, which mark their territories by scratching as high as they can on tree trunks, a signal physically connected to their size (Thapar 1986). It has also been hypothesised that visual marks simply identify the location of chemical signalling (Burst and Pelton 1983). However, we believe that this may not always be the case, since: (1) visual marks do not necessarily happen on trees where body rubbing and pedal marking occur (Supplementary Data Figures 1 and 9); and (2) a visual mark on a tree in a forest is only visible when the receiver is close to the mark, whereas chemical signals may go farer (e.g. by wind action) and reach an animal before a visual one.

Our results suggest that trunk debarking by brown bears plays an important role in visual communication at least during the mating season. In turn, visual signalling may be related to individual fitness, because communication is the first step towards successful mating and eventual reproduction.

This is the first time, to our knowledge, that the active role of visual marking in a mammalian species was experimentally tested in the field. To conclude, bear reactions to our manipulation suggest that visual signalling could represent a widely overlooked mechanism in mammal communication, which may be more broadly employed than was previously thought.

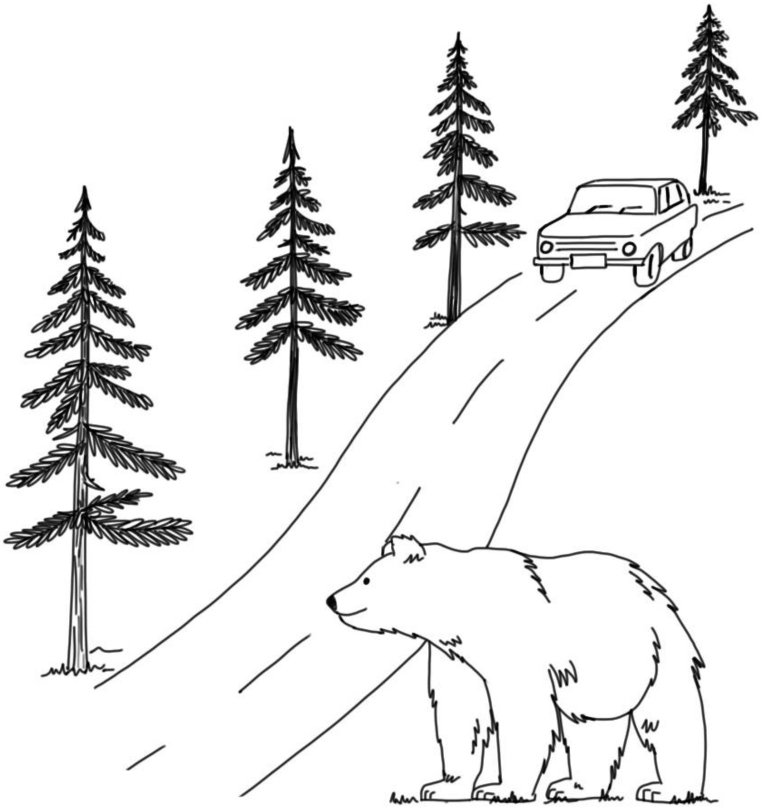
## Supplementary Data

Due to the length and size of the photos and videos included in Supplementary Data, this material can be accessed through the following link:

https://drive.google.com/drive/folders/101MpTURt87hZoG4Drdz1MorvH5-fbES8?usp=sharing

# *Chapter V*

# The influence of road networks on a large carnivore spatial distribution and habitat suitability in a human-modified landscape



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## SUMMARY

Roads are human infrastructures that heavily affect wildlife, often with marked impacts on carnivores, including brown bears *Ursus arctos*. Yet, little information exists for European brown bears. In this study, we assessed the potential impact of road networks on the distribution of brown bears in the small, isolated and endangered population of the Cantabrian Mountains (North-western Spain). To study whether road networks affect brown bear spatial distribution, we first assessed the variables that determined the distance of the bears to the nearest road, including traffic volume and road visibility, i.e., if we expected that surrounding roads were visible to bears. Second, we built two sets of habitat suitability models, both with and without roads, to discern the possible loss of habitat suitability caused by roads. Mean distance of bear locations to the nearest road was 968 ± 804 m and the closest road was a low traffic road in 72.5% of all bear locations. With the exception of terrain roughness, the whole set of parameters that we have taken into account in our analyses showed little influence on the bear distance to the nearest road. Habitat suitability models showed small effect of the road networks in our study area on brown bear habitat suitability. However, it is important to highlight here that only a low proportion (16.5%) of the cells classified as bear suitable habitats were crossed by roads, e.g., most of the roads are mostly located in bear unsuitable habitats in the Cantabrian Mountains. Our results seem to support the possibility that road networks in the Cantabrian human-modified landscape have low impact on the spatial occurrence of brown bears. Compared to previous studies conducted in other populations, mainly North American ones, our findings may suggest a different response of Eurasian brown bears to roads due to a longer bear-human coexistence in Europe versus North America. Our approach may represent a first step to detect potential habitat loss in bear distribution and where road networks may impact more

at a spatial level. However, the apparent road tolerance indicated by indirect approaches does not exclude other detrimental effects, e.g., road mortality due to collision, stress increase and movement pattern disruption, only detectable by more direct approaches.

## INTRODUCTION

Roads are one of the most ubiquitous human infrastructures, which have frequently shown to have crucial effects on wildlife (Zeller et al. 2020). Road networks can: (a) affect surrounding ecosystems by increasing pollutants due to vehicle traffic (Forman et al. 2003); (b) facilitate the arrival and spread of non-native species (Schowalter 1988; Watkins et al. 2003); (c) allow human access to previous pristine areas (Steyaert et al. 2016; Lamb et al. 2018); (d) modify ecological communities (Trombulak and Frissel 2000); (e) fragment and/or destroy habitats (Forman et al. 2003; Riitters et al. 2004; Coffin 2007); (f) increase wildlife mortality (Penteriani et al. 2018; Morales-González et al. 2020); and (g) represent barriers to movement that may reduce population viability and gene exchange (Shepard et al. 2008; Holderegger and Di Giulio 2010; Epps and Keyghobadi 2015). Moreover, these effects vary depending on road type and consequent traffic loads (Koreň et al. 2011; Northrup et al. 2012; Chen and Koprowski 2019), which may modify animal behaviour (Barber et al. 2010; Morales-González et al. 2020), habitat selection, parental investment (Frid and Dill 2002), and increase energetic costs and physiological stress of animals (Wasser et al. 2011; Houston et al. 2012; Jacobson et al. 2016).

Wide-ranging mammals with low reproductive rates and low densities (e.g., large carnivores) are particularly vulnerable to the multivariate effects of roads and vehicle traffic (Alexander et al. 2005; Rytwinski and Fahrig 2015). For example, roads can negatively impact tiger *Panthera tigris* survival and reproductive rates (Kerley et al. 2002), and influence movement behaviour through road avoidance of jaguars *Panthera onca* (Colchero et al. 2011) and wolves *Canis lupus* (Ciucci et al. 2018; Dennehy et al. 2021). Indeed, fragmentation of carnivore populations caused by roads (Fahrig and Rytwinski 2009) can affect the functioning of the entire ecosystems due to the ecological role of large carnivores as apex predators (Ordiz et al. 2013, 2014).

Among large carnivores, the multiple, non-exclusive effects of roads on brown bears *Ursus arctos* have been extensively studied, mainly in North America. For example, avoidance patterns (Proctor et al. 2020; Støen et al. 2020) and fast displacement rates (Roever et al. 2010; Kite et al. 2016) have been described in road surroundings, with bears selecting higher elevation and steeper slopes because they are further away from road and, consequently, less accessible to humans (Nams et al. 2006; Goldstein et al. 2010). Habitats surrounding roads and periods of the bear cycle also seem to have an important role on the impact of road networks, higher probabilities of crossing roads being related to those intersecting habitats offering shelter (Roever et al. 2010; Lyons et al. 2018; Find'o et al. 2019) or during hyperphagia (Stewart et al. 2013; Frąckowiak et al. 2014), due to the need to high intake of food before hibernation. Along the same line, some age classes such as females with cubs and subadults can positively select roads to avoid risky encounters with adult males (Graham et al. 2010; Penteriani et al. 2018). Moreover, the traffic volume associated with the type of road has also been shown to determine the severity of road impacts on bears (Elfström et al. 2008; Northrup et al. 2012). Actually, increasing traffic intensities are often associated with stronger avoidance (Mace et al. 1999; Jacobson et al. 2016), decreasing permeability (Skuban et al. 2017; Find'o et al. 2019), affecting movements rates (Roever et al. 2010; Proctor et al. 2012) and altering rhythms of activity (Waller and Servheen 2005; Støen et al. 2020). Finally, one aspect of roads that might affect bears, and which has never taken into account before in bears, is road visibility or viewshed, i.e., the part of the environment assumed to be visible to an animal in a given position (Tandy 1967). Actually, in recent years, it has been advocated that the quantification of animal potential visual space may improve the understanding of animal comfort in the environment (Aben et al. 2018), but still few examples exist on the link between viewshed ecology and large carnivores (Grant et al. 2005; Davies et al. 2016).

Here, we first assessed the impact of the road network on the spatial distribution of brown bears in the small, isolated, and endangered population inhabiting the human-modified landscape of the Cantabrian Mountains (NW Spain). We hypothesised that distance of bears to roads should be shorter: (1) when individuals are in areas with shelter (e.g., forest cover) compared to open habitats; (2) when bear locations were assumingly not in view of the road, as approximated by a viewshed (see Methods); (3) if the traffic level is low; (4) for females with cubs during the mating season because of the risk of infanticides (Steyaert et al. 2020); and (5) during hyperphagia, as bears may use food resources associated with roads edges (Penteriani et al. 2018). Further, and with a modelling exercise, we tested the possibility that road networks may reduce habitat suitability for bears, an effect that we expect might act differently depending on bear classes and seasonal cycles (Penteriani et al. 2018; Morales-González et al. 2020).

## METHODS

### Study area

The study area encompasses the distribution range of the Cantabrian brown bear population in the regions of León, Palencia and Asturias provinces, NW Spain (Figure 1). It extends along the Cantabrian Mountains with an average altitude of 1100 m a.s.l. (maximum 2650m). The climate of the region is oceanic, more continental and dryer along southern slopes and temperate and more humid in northern slopes (Ortega and Morales 2015). Landscape of the region is mainly covered with forests, shrublands and farmlands. The forests of the southern slopes are mainly composed by semi-deciduous and evergreen oaks (*Quercus sp.*), whereas the northern slopes host mostly deciduous forests (*Fagus sylvatica*; *Q. robur*, *Q. petraea*; *Betula sp.*; (García de Celis et al. 2004;

Mateo-Sánchez et al. 2016)). Non-forested areas are covered with shrubs such as brooms (*Cytisus sp.*) and heather (*Erica sp., Calluna sp.*), while above the tree line, berry shrubs as bilberries appear (*Vaccinium myrtillus*) (Pato and Obeso 2012; Mateo-Sánchez et al. 2016). Most bear habitat patches are embedded in a matrix of urbanized and cultivated areas with a high density of transport routes and human settlements, where the main economic activities are livestock breeding, recreational activities, mining and timber harvesting (Zarzo-Arias et al. 2019).

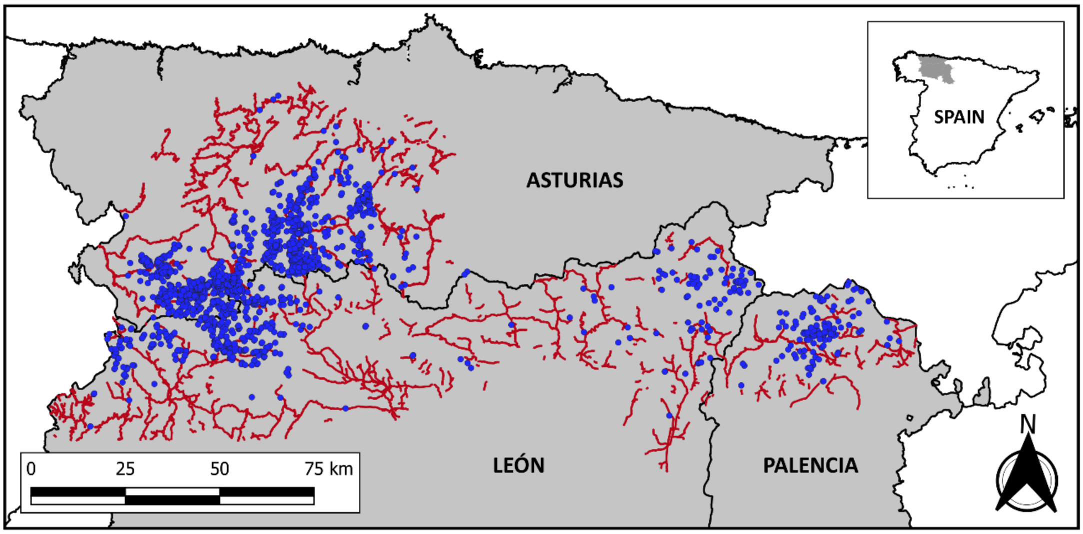


**Figure 1**. Bear locations and road sections included in the study located in the Cantabrian Mountains (NW Spain; provinces of Asturias, León and Palencia). The 2722 bear locations are represented as blue dots, and road sections are shown as red lines. Due to the short distance that separates roads, only road sections of Types 2 and 3 (those with more traffic intensity, see Methods section) are represented. Inset shows location of mapped area within the geographic limits of peninsular Spain.

## Bear dataset

The locations of brown bears used for this study (n= 2722) were collected from 2000 to 2016 and were compiled from: (1) georeferenced direct sightings and footprints (n = 2722 locations) taken by the staff of the Junta de Castilla y León and Principado de Asturias, primarily by the Patrulla Oso, (i.e., Bear Patrol), as well as by all the other field personnel of both regional governments and NGO's (Fund for the Protection of Wild Animals (FAPAS); Asturias Bear Foundation (FOA); and Brown Bear Foundation (FOP); (2) camera traps randomly placed by the FAPAS and Bear Patrol during the last 20 years, mainly in forested areas where bears are less visible, and (3) personal observations (direct sightings and footprints) of the authors. The bear sightings on which this study is based were both the result of systematic and random observations. Each observation was accompanied by information on the date and the age class of the sighted bears, i.e., adult or subadult, unknown lone bears, female with cubs, female with yearlings. We classified the bear locations into three seasons, accordingly to the annual cycle of this population: denning (January 1 to April 15), mating (April 16 to June 30), and hyperphagia (July 1 to December 31) (Zarzo-Arias et al. 2020). Due to the mild winters of the area, food is available also during winter, and not all bears in this population hibernate (González-Bernardo et al. 2020).

## Model covariates

On the basis of the information obtained from previous studies on this bear population (Lamamy et al. 2019; Zarzo-Arias et al. 2019), we selected those variables (land use, season, bear class, traffic volume and road visibility; Tables 1.a-1.b) that may have an effect on the distance of bears to the nearest road (hereafter, NR), as well as some additional topographic variables (altitude, slope and terrain ruggedness). The variable land use was extracted from the CNIG (Environmental Thematic Cartography of the Principality of Asturias; Sheets of the Map of Vegetation, Lithology, Rocks and Habitat of the Bear. 2011. Scale 1:25000. © Principado de Asturias, Spain) and reclassified into seven land cover types: (1) forests, (2) shrubs, (3) pastures, (4) farmlands, (5) rocky areas, (6) bare ground/water and (7) urban areas. The first six land uses were used in the construction of the distance to roads models (see Road network effects on brown bear spatial distribution section), while for the habitat suitability analyses we also included the urban areas (see Potential impact of road networks on brown bear habitat suitability section).

**Table 1.a.** List of the numerical variables included in the models, their description and mean, minimum and maximum values.

| Variable code | Description | mean | SD | min | max |
|---|---|---|---|---|---|
| ***dnear*** | Distance to the nearest road. | 968.1 | 804.0 | 0.1 | 4594.3 |
| ***alti*** | Altitude above the sea level | 1176.0 | 351.16 | 107.6 | 2207.3 |
| ***slo*** | Slope (%) | 59.7 | 22.95 | 0.1 | 147.2 |
| ***rugg*** | Ruggedness index | 1272.8 | 1592.16 | 2.2 | 9962.2 |

**Table 1.b.** List of non-numerical variables included in the models, their description and counting by levels within each variable.

| Variable code | Description | values | N |
|---|---|---|---|
| ***year*** | Year of observation | 2000 - 2016 | 2722 |
| ***class*** | Class of bear | 1 (Adult/subadult lone bears) | 1441 |
| | | 2 (Female with yearlings) | 201 |
| | | 3 (Female with cubs) | 1080 |
| ***season*** | Period of the bear lifecycle | 1 (Mating, 16th april – 30th June) | 1122 |
| | | 2 (Hyperphagia, 1st July – 31st December) | 1045 |
| | | 3 (Denning, 1st January – 14th April) | 555 |
| ***luse*** | Land use (land cover) | 1: Forests | 1420 |
| | | 2: Shrubs | 788 |
| | | 3: Pastures | 149 |
| | | 4: Farmlands | 155 |
| | | 5: Rocky areas | 179 |
| | | 6: Bare ground/water | 31 |
| ***vis_near*** | Visibility of the nearest road | 1 (visible) | 1855 |
| | | 0 (no visible) | 867 |
| ***type_near*** | Type of nearest road (by traffic intensity, IMD) | 1:IMD: 0-337 vehicles/day | 1974 |
| | | 2: IMD: 338-1411 vehicles/day | 426 |
| | | 3: IMD: 1412-5129 vehicles/day | 322 |

The road layer of the study area was obtained from the CNIG, and the closest road and the closest visible road were selected for each bear location. These roads were classified into 3 groups based on the average daily volume of traffic, with data obtained from the public repositories of the Spanish Ministry of Public Works and Transport (MITMA, https://www.mitma.es/carreteras), Castilla y León government (Junta de Castilla and León, https://carreterasytransportes.jcyl.es/web/es/carreteras-transportes.html) and Principado de Asturias government (SADEI, https://sadei.es/inicio). The unit of the traffic volume was the daily traffic intensity (IMD; i.e., vehicles/day, hereafter, v/d), taking as the value for each road the mean value of the average monthly IMD of the years from 2012 to 2018, as these are the years with the most complete and modern data. The types of roads based on the IMD were established according to the 'natural breaks' method, which is based on the nature of the data and identifies important jumps in the sequence of values, optimizing the grouping of similar values and maximizing the differences between classes (Jenks 1967). The road types for the roads considered according to the ranges of IMD values established by the method are the following: Type 1 = 0 - 337 v/d; Type 2 = 338 - 1411 v/d; and Type 3 = 1412-5129 v/d.

The topographic variables and viewsheds were calculated from a Digital Elevation Model (DEM) and a Digital Surface Model (DSM), respectively. Both models have a 30m resolution and are based on a LiDAR (Light Detection and Ranging) data layer obtained from the Spanish Geographic National Institute (CNIG; https://centrodedescargas.cnig.es/CentroDescargas/index.jsp), which has a minimum density of one point every two meters and an altimetry precision of 15-20 cm. This allows the calculation of highly accurate DEMs and DSMs and consequently, the derivation of more precise viewsheds (Aben et al. 2018; Lagner et al. 2018). These viewsheds incorporate elements of the physical environment that may interfere with the field of vision of the observers (e.g., vegetation, topographic features or infrastructures).

For the calculation of the viewsheds and the analysis of visibility, a raster of visible cells of the DSMs from one or more bear locations was calculated, with a range of 1000m (visible cells = 1, non-visible cells = 0). That MDS takes into account the real height of the vegetation and of the topographic elements, through point clouds with three-dimensional coordinates obtained by airborne LiDAR sensors (Lorite et al. 2015). As far as we know there are no published data on the visual range or acuity of brown bears. However, different thresholds of proximity to roads have been described in which road avoidance can be detected, most of them being at least 500 m (McLellan 1989; Mace et al. 1996; Waller and Servheen 2005; Torres et al. 2016). We decided to set our road visibility threshold at least twice that the distance proposed for grizzly bears, on a conservative principle. Next, based on this and the road type raster layers, we calculated through a map algebra process a third raster layer with the road type information and its visibility for each road section visible 1 km from each bear location. On this layer, the visible road sections acquired values 1 to 3 depending on the type of road, getting a value of 0 for the non-visible ones. We then calculated the distance from each bear location to the NR, which represents our response variable. All spatial variables (topographic, land use, visibility and distance to roads) were analysed using ArcGIS 10.5 software (ESRI, Redlands, USA).

## Statistical analysis

### Road network effects on brown bear spatial distribution

We built a lineal mixed model with the distance of each bear observation to the NR (*dnear*) as a response variable and the variables described above (see Model covariates section) as predictors. We log-transformed the response variable to approximate normality in the residuals, and re-scaled the numeric explanatory variables to mean = 0 and standard deviation = 1, in order to standardize their values. To account for spatial autocorrelation of bear presence data, we included in our model the autocovariate (*ac*) through the *spdep* package (Bardos et al. 2015; Bivand et al. 2019). To exclude collinearity among the predictors, we calculated the variance inflation factor (VIF; Belsley et al. 2005) but no variable exceeded VIF=2 (maximum VIF=1.57). Models were built using the lme4 package (Bates et al. 2015). Model generation and model averaging (models with ΔAICc <2) were performed using the MuMIn package (Bartoń 2013). Using Akaike's Information Criterion corrected for small sample sizes (AICc) and according to AIC-driven model selection, a random year in the model was not judged necessary. Models were run in R v. 3.5.1 statistical software (R Foundation for Statistical Computing 2018).

For the scope of our model, we assessed if our dataset of direct sightings, which comprised most of the location data, was biased toward open areas by comparing the same model built with and without direct sightings. As both models produced comparable results, we believe observational bias, if any, has a negligible effect on the model performance. To discard a bias towards open terrain deriving from our data (consisting mainly on direct sightings) we built a model with direct observations and another with only locations based on footprints, which are not biased by detectability since they are not more easily detectable in open terrain. Although the second model had few observations (n = 189), we observed similar trends and responses of the variables, thus discarding biases and we built the distance to-road models with all the observations.

### Potential impact of road networks on brown bear habitat suitability

To assess habitat suitability for brown bears according to the study area road network, we used the software MaxEnt version 3.3.3k called from the R environment version

3.5.1 with the packages dismo version (Hijmans et al. 2017) and ENMeval version (Muscarella et al. 2014) following the methodology applied in Zarzo-Arias et al. (2019). To identify an optimal model structure for each input bear dataset, we evaluated candidate models with all types of feature combinations, each run over a set of regularization multipliers ranging from 0 to 19 (for more detailed information see Zarzo-Arias et al. (2019)). We included the same variables as in the previous lm model (land use, altitude and slope) and the variable *dnear*, but removed ruggedness due to its high correlation with slope. Following the aforementioned methodology, we have also included urban area as an additional land use, not represented in the distance to-road models (Supplementary Table S1). We made a model for each bear class in each season except for females with yearlings in hyperphagia as we only had 4 occurrence locations. We used 5000 iterations, a convergence threshold of $10^{-5}$, 50 replicates and centre coordinates from all cells in the study area to build the models.

We identified the best combination of feature types and regularization multiplier using AICc We considered models within 2 AICc units of each other to have equivalent empirical support (Anderson and Burnham 2004) and chose the simplest as the best model (the one with the lowest number of parameters, and if equivalent, the one with the lowest number of feature types) (Supplementary Table S2). We obtained the output maps of the best model for each group with the complementary log-log (cloglog) format, which allows interpreting values given to each cell from 0 to 1 as a probability of bear occurrence.

We extracted all cells crossed by a road for each bear type in each season and analysed their occurrence probability (MaxEnt cloglog values). For selecting a threshold to identify most suitable bear range, we extracted for each bear class occurrence locations used to build the models the values predicted by their corresponding model and calculated the mean of values predicted by the model for all bear occurrence points, which was 70% of probability of bear occurrence (cloglog value = 0.7, Supplementary Table S3). We select this value as threshold, and finally we compared cells above that threshold with the type of the closest road (see Model covariates section).

## RESULTS

More than half (52.9%) of the bear locations corresponded to lone bears, 39.7% to females with yearlings and 7.4% to females with cubs. Observations were more frequent during the mating and hyperphagia seasons (41.2 and 38.4%, respectively), followed by locations recorded during the denning season (20.4%). Most of the bear locations occurred within forests (52.2%) and shrubs (28.9%) and, to a lesser extent, rocky areas (6.6%), farmlands (5.7%) and pastures (5.5%). In relation to the bear distance to NRs, most locations (72.5%) occurred next to low-traffic roads of Type 1, followed by Type 2 (15.7%) and Type 3 (11.8%) roads. The mean distance (± SD) of bear locations to NRs was 968 m ± 804 m (min. = 0 m, max. = 4595 m) (see Tables 1.a-1.b.).

### Road network effects on brown bear spatial distribution

The most parsimonious model (Supplementary Table S4) included all the variables considered, except roughness (Table 2). Considering the percentage of variance explained by each variable, the altitude had the strongest effect ($R^2 = 0.34$), with the bear distance to NR increasing with altitude. All the other variables showed weak effects (Supplementary Figures S1.1-S1.8). Bear distance to NR was lower in lower slopes and when the road was supposedly not visible from the animal position. Also, distance to NR was lower in farmlands, pastures and bare ground than in forests. In mating season, bears were located further from roads, mainly lone individuals. Finally, distances to NR were lower in presence of Type II than for Type I roads.

**Table 2**. Effects of explanatory variables on brown bear distance to the NR in the Cantabrian Mountains (n = 2722 locations). For each explanatory variable, we report the estimate (β), standard error (SE), significance (p), confidence intervals (CI) and explained variance ($R^2$) obtained from model averaging on the models with ΔAICc < 2. Baseline level for categorical variables are: "forests" for land use, " lone bears" for class of bear, "mating" for season, “type 1” for type of the NR and "not visible" for visibility of the NR. The most important parameters are highlighted in bold.

| ***Dependent variable*** | ***Explanatory variable*** | ***Model-averaged coefficients and relative importance values*** | | | | |
|---|---|---|---|---|---|---|
| | | **β** | **SE** | **p** | **CI** | **$R^2$** |
| **Distance to the nearest road** | Intercept | 6.872 | 0.033 | <0.001 | (6.806; 6.937) | - |
| | **Altitude** | **0.494** | **0.013** | **<0.001** | **(0.469; 0.520)** | **0.346** |
| | Bear Class #2: FWYs | -0.193 | 0.049 | <0.001 | (-0.289; -0.097) | 0.006 |
| | Bear Class #3: FCOYs | -0.070 | 0.026 | 0.007 | (-0.120; -0.019) | 0.003 |
| | Landuse #2: Shrubs | -0.066 | 0.029 | 0.022 | (-0.123; -0.009) | 0.002 |
| | Landuse #3: Pastures | -0.242 | 0.056 | <0.001 | (-0.351; -0.132) | 0.007 |
| | Landuse #4: Farmlands | -0.331 | 0.054 | <0.001 | (-0.437; -0.225) | 0.014 |
| | Landuse #5: Rocky areas | 0.007 | 0.051 | 0.881 | (-0.092; 0.107) | 0.000 |
| | Landuse #6: Bare ground/water | -0.525 | 0.115 | <0.001 | (-0.750; -0.300) | 0.008 |
| | Season #2: Hyperphagia | 0.148 | 0.028 | <0.001 | (0.093; 0.203) | 0.010 |
| | Season #3: Winter/denning | 0.243 | 0.034 | <0.001 | (0.175; 0.310) | 0.018 |
| | Slope | 0.092 | 0.013 | <0.001 | (0.066; 0.117) | 0.018 |
| | Type of the NR: Type #2 | -0.238 | 0.035 | <0.001 | (-0.305; -0.170) | 0.017 |
| | Type of the NR: Type #3 | -0.038 | 0.038 | 0.321 | (-0.113; 0.037) | 0.000 |
| | Visibility of the NR: Visible | -0.270 | 0.028 | <0.001 | (-0.325; -0.216) | 0.034 |

Potential impact of road networks on brown bear habitat suitability

Slope showed the highest proportional contribution to all models, followed by altitude and forests. Models including the variable distance to NR performed similarly compared to models that did not include this variable, although its contribution to the models was generally low (< 1.5%), denoting a low impact of roads proximity on bear habitat suitability (Supplementary Table S6, Supplementary Figures S2.1-2.8). On the other side, the model of females with yearlings during the denning season showed a higher contribution of the variable distance to NR (13.4%). In general, all bear classes have a weak positive relationship with the distance to roads in each season (Supplementary Figures S3.1-3.8).

Cells crossed by a road were not classified by the models as highly suitable habitat for bears (less than 16.5% of those cells had more than 70% probability of bear occurrence, Supplementary Table S6, Figure 2). Despite this, both the models that included the distance to NR variable and those that did not include it presented similar habitat suitability. Actually, the maximum difference in percentage of high suitable grids (>70% probability of presence) crossed by a road between models with and without distance to roads is less than 2%.

## DISCUSSION

The two approaches used here to explore the potential impacts of road networks on the spatial distribution of brown bears belonging to a population inhabiting a human-modified landscape suggest that roads do not alter bear spatial distribution and/or habitat suitability.

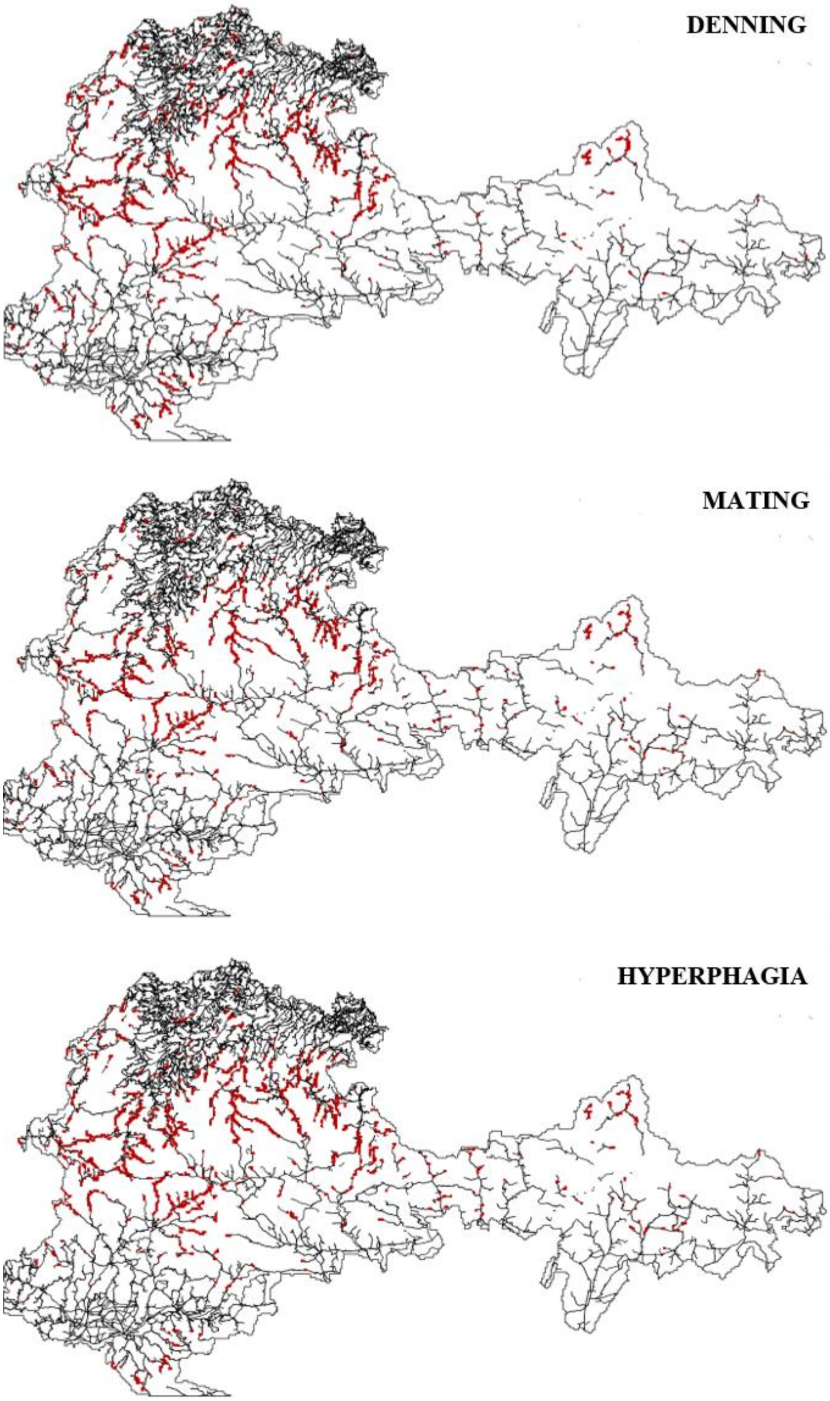


**Figure 2**. Map of the average probability value predicted by MaxEnt of all bear classes in each season showing cells above the cloglog MaxEnt value of 0.7 (70% probability of bear occurrence) which intersect with a road (sections in red), and thus, representing roads crossing high suitability habitats for the brown bears in the Cantabrian Mountains.

Several studies have previously described roads as a factor affecting brown bear behaviour, spatial distribution, and habitat use, either by analysing the bear distances to the roads or by quantifying the density of road networks. However, in our study we found that a large part of the variation in the distance to nearest roads is explained by altitude. Taking into account the characteristics of the study area, where roads are prevalently located in valley bottoms, this relationship seems to be circumstantial since brown bears tend to be more frequently located in higher areas due to avoidance of human settlements and infrastructure in valley bottoms (Goldstein et al. 2010; Frąckowiak et al. 2014). This possible explanation is also supported by the fact that altitude and distance to nearest road presented a substantial Pearson's correlation (0.58) in our habitat suitability models.

Contrary to our expectations, neither the habitat type nor the visibility of the nearest roads seem to affect significantly brown bear distance to nearest road. Moreover, our habitat suitability models were not affected by the inclusion of roads, except for the model that considered females with yearlings in the denning season. Without forgetting the low sample size of this model (n = 93), we suggest that the impact of roads on the habitat suitability of females with yearlings during this season may be due to their higher activity compared to other bear cohorts that are usually hibernating. In the southernmost populations and with mild winters, many bears do not hibernate, with the exception of pregnant females and females with yearlings have been reported to hibernate less than other bear classes (González-Bernardo et al. 2020b). Additionally, as the habitat suitability models show, road surroundings are frequently characterised by low suitability, probably because less favourable habitats (i.e., farmlands) and human settlements and activities surround roads. Finally, visibility of the nearest roads is related to the type of habitat in which they are located. It has been reported how bears near roads preferentially use mature and dense forests at daytime, which would limit their visibility (Roever et al. 2010). Gibeau et al. (2002) and Roever et al. (2008a) observed that Canadian brown bears were closer to roads, or were likely to cross them, if there were high quality habitats around them. It has been suggested that closeness to roads may be related to the presence of attractive food (Stewart et al. 2013; Morales-González et al. 2020), especially in spring and early summer (Roever et al. 2008b), as well as during hyperphagia (Graham et al. 2010; Zarzo-Arias et al. 2018). Yet, as roads increase mortality rates (Bourbonnais et al. 2014; McLellan 2015), vehicle networks represent sink-like areas (Falcucci et al. 2009; Braid and Nielsen 2015) or ecological/evolutionary traps (Ciarniello et al. 2007; Penteriani et al. 2018).

The distance to nearest road seems to be little dependence on bear classes. Brown bear sex and age classes have previously been described as showing different patterns of road avoidance and crossing, but they seem to be dependent on local features because described patterns are not consistent between studies (e.g., Gibeau et al. 2002; Chruszcz et al. 2003; Waller and Servheen 2005; Roever et al. 2008b; Graham et al. 2010; Steyaert et al. 2016; Proctor et al. 2018). Actually, the lack of uniformity of sex and age responses to road networks may be due to the local features of habitats surrounding roads, which would offer different trophic resources and/or shelter throughout the year (Morales-González et al. 2020). For example, females with subs can select for areas close to roads as a mechanisms of adult male avoidance to prevent infanticides (Graham et al. 2010; Penteriani et al. 2018, but see Waller and Servheen 2005).

Considering previous studies on the effects of road networks in other brown bear populations in Europe and North America, the observed different response of the species between these two continents stands out. Actually, roads showed a more marked negative effect in North American populations (Morales-González et al. 2020;

but see Güthlin et al. 2011 and Frąckowiak et al. 2014). The historical coexistence of humans and brown bears in Europe, contrasts with the shorter and more intense interaction experienced by North American populations, where widespread human presence and activities are much more recent (Fortin et al. 2016; Støen et al. 2020). In Europe, human density and encroachment is also higher than in North America (Swenson et al. 2000; Fortin et al. 2016). Thus, different levels of exposure to human activity and persecution may have motivated the observed different behavioural responses (Ordiz et al. 2014; Morales-González et al. 2020). Actually, in a previous study on this Cantabrian population, it has been recorded that bears seem not to modify their surveillance behaviour with respect to the distance to roads (Zarzo-Arias et al. 2018). In other European populations: (a) bear occurrence was positively related to distance to roads in the Italian Central Apennines (Maiorano et al. 2019); (b) lack of habitat avoidance/attraction was recorded near roads in Slovenia (Kaczensky 2000; Kaczensky et al. 2003); (c) habitat selection in the reintroduced population of brown bears in the Pyrenees was not affected by road density (Martin et al. 2012); and (d), the proximity of roads in Romania seemed not to affect bear activity (Roellig et al 2014). Thus, our approach seems to suggest that traffic intensity did not explain the distance to nearest roads in the Cantabrian Mountains, despite the expected avoidance depending on the traffic level that has been recorded otherwise in Europe (Huber et al. 1998; Kaczensky et al. 2003; Skuban et al. 2017; Find'o et al. 2019). We suggest that in our study area, prevalently mountainous and without large urban areas, levels of vehicle traffic might not reach the avoidance threshold that makes bear sensitive to road presence.

On the contrary, in North America (mainly British Columbia and Alberta in Canada and Alaska and Montana in the U.S.), greater avoidance of the area adjacent to roads has been reported (McLellan 1989; Waller and Servheen 2005; Ciarniello et al. 2007). This negative selection of habitats near roads has been described either regardless of traffic (McLellan and Shackleton 1988; Jacobson et al. 2016) or as a traffic-dependent phenomenon (Mace et al. 1996, 1999; Gibeau et al. 2002; Chruszcz et al. 2003; Northrup et al. 2012; Proctor et al. 2012), with low frequencies of road crossing when traffic level increases (Chruszcz et al. 2003; Waller and Servheen 2005). Faster movements and lower activity rates have also been described (Roever et al. 2010; Proctor et al. 2012), as well as more nocturnal behaviour (Waller and Servheen 2005; Northrup et al. 2012). The difference between Europe and North America thus evidence that projecting management or mitigation measures at the same spatial scales for Europe and North America might not be appropriate due both to the different sensitivity that bears on both continents seem to exhibit to roads and to the different degree of landscape human modification and encroachment.

Because discerning the role of road networks in large carnivore ecology is crucial, particularly relevant in isolated and small populations like the Cantabrian one, we consider important to stress here the main limitation of our approach. This work is based on opportunistic observations and indirect evidences, which do not provide as accurate information about individual movements and rhythms of activity around roads, as well as potential road avoidance strategies, as telemetry does. Similarly, proposals for road mitigation measures (e.g., green bridges and viaducts) should be based on telemetry studies, not only on distribution data. In populations inhabiting highly humanized territories since centuries such as the one studied, the scale and entanglement level of human activities in the bear habitat should always be taken into account.

# Supplementary Data

**Supplementary Table S1.** Mean values of each environmental variable included in the MaxEnt models in the cells crossed by the different types of roads. Altitude values are indicated in meters, while the values of the different land uses represent percentages.

| *Type of road* | *Altitude* | *Bare areas* | *Farmlands* | *Forest* | *Pasture* | *Rocks* | *Shrubs* | *Slope* | *Urban areas* |
|---|---|---|---|---|---|---|---|---|---|
| **1: low traffic** | 703.21 | 2.27 | 32.54 | 31.17 | 6.06 | 1.09 | 18.39 | 8.24 | 2.11 |
| **2: medium traffic** | 839.92 | 2.15 | 27.23 | 32.74 | 9.97 | 1.57 | 15.30 | 8.05 | 2.62 |
| **3: high traffic** | 888.36 | 2.07 | 26.51 | 31.24 | 15.86 | 1.68 | 12.34 | 6.81 | 3.09 |
| **All roads** | 836.11 | 2.65 | 26.60 | 31.79 | 11.18 | 1.60 | 16.78 | 7.76 | 2.11 |

**Supplementary Table S2.** Description of the best models for each bear class in each season. * means that there was more than one model within 2 units of ΔAIC from the best one and thus, the selected model was the simplest (less number of parameters, and if the same, less number of features and regularization multiplier). fcmat = females with cubs during mating; fchyp = females with cubs during hyperphagia; fcden = female with cubs during denning; fymat = females with yearlings during mating; fyden = females with yearlings during denning; omat = other bears during mating; ohyp = other bears during hyperphagia; oden = other bears during denning.

| *Model* | *Features* | *rm* | *AICc* | *ΔAIC* | *Parameters* |
|---|---|---|---|---|---|
| **Fcden** | LQP | 13 | 2388.5468 | * | 17 |
| **Fcmat** | LQHP | 3 | 6675.1238 | * | 42 |
| **Fchyp** | LQPT | 2 | 6438.6357 | 2.8569 | 47 |
| **Fyden** | LQ | 1 | 1641.9436 | * | 14 |
| **Fymat** | LQH | 4.5 | 1801.7626 | * | 13 |
| **Oden** | LQ | 1 | 4383.1987 | * | 18 |
| **Omat** | LQHPT | 2.5 | 8479.3350 | 4.0518 | 43 |
| **Ohyp** | LQHPT | 2.5 | 10572.1851 | 7.7639 | 51 |

**Supplementary Table S3.** Mean habitat suitability values predicted by the models of each bear class in each season and for all bear occurrence points. fcmat = females with cubs during mating; fchyp = females with cubs during hyperphagia; fcden = female with cubs during denning; fymat = females with yearlings during mating; fyden = females with yearlings during denning; omat = other bears during mating; ohyp = other bears during hyperphagia; oden = other bears during denning.

| Model | Mean habitat suitability |
|---|---|
| **fcden** | 0,6498 |
| **fcmat** | 0,6596 |
| **fchyp** | 0,6624 |
| **fyden** | 0,6250 |
| **fymat** | 0,6610 |
| **oden** | 0,6415 |
| **omat** | 0,6548 |
| **ohyp** | 0,6523 |
| **all models** | 0,6508 |

**Supplementary Table S4.** Unique competing model (ΔAICc <2) from LMs built to investigate variables influencing distance to NRs in the Cantabrian brown bear population. Adjusted R-squared of the most parsimonious model is 0.445. Variable codes: alti = altitude above the sea level, slope = slope (%), class = class of bear, season = period of the bear lifecycle, luse = land use (land cover), type_near = type of NR (by traffic intensity, IMD), vis_near = visibility of the NR.

| ***Dependent variable*** | ***Competing models*** | ***df*** | ***AICc*** | ***ΔAICc*** | ***Weight*** |
|---|---|---|---|---|---|
| Distance to the nearest road | alti + slope + class + season + luse + type_near + vis_near | 17 | 5180.80 | 0.00 | 0.73 |

**Supplementary Table S5.** Percent of contribution of each of the variables to the MaxEnt models (r: including distance to NR, nr: not including it) for each bear class in each season. The variable distance to NR is highlighted, and the model in which it contributed the most (females with yearlings in denning) is in bold. fcmat = females with cubs during mating; fchyp = females with cubs during hyperphagia; fcden = female with cubs during denning; fymat = females with yearlings during mating; fyden = females with yearlings during denning; omat = other bears during mating; ohyp = other bears during hyperphagia; oden = other bears during denning.

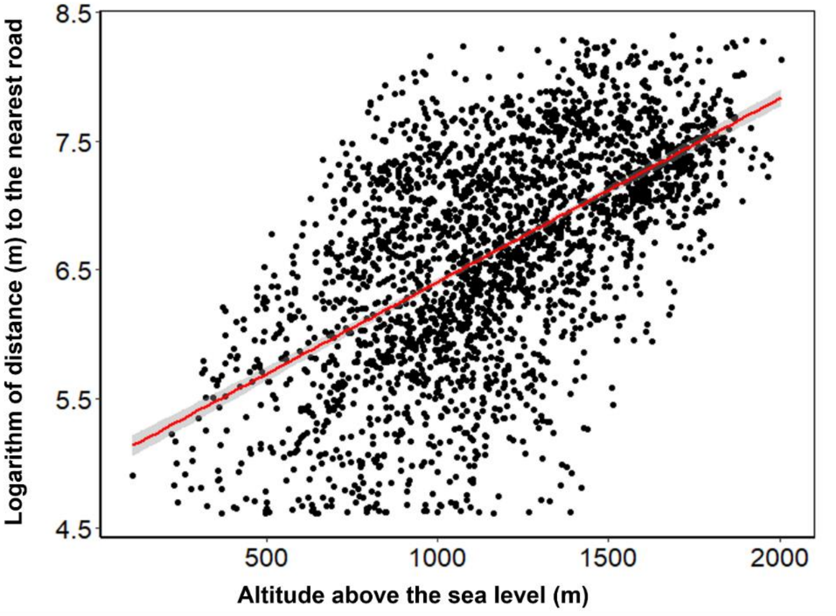
| ***Variables*** | **fcden** | | **fcmat** | | **fchyp** | | **fyden** | | **fymat** | | **oden** | | **omat** | | **ohyp** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** |
| **Dist. to the nearest road** | **0.2** | **-** | **1.5** | **-** | **x** | **-** | **13.4** | **-** | **3** | **-** | **0** | **-** | **0.8** | **-** | **0** | **-** |
| **Altitude** | 4.9 | 5.9 | 3.9 | 4 | 3.5 | 3.5 | **3.3** | **10.5** | 1.2 | 1.3 | 5.7 | 4.5 | 9.2 | 8.5 | 13.1 | 14.4 |
| **Bare areas** | 0.1 | 0 | 1.7 | 1.2 | 0.2 | 0.3 | **2.5** | **2.8** | 5.8 | 6.4 | 0.4 | 0.6 | 0.7 | 0.3 | 0.1 | 0.5 |
| **Farmlands** | 2.3 | 1.5 | 3.2 | 2.9 | 8.2 | 7.3 | **9.4** | **8.7** | 2 | 1.8 | 5.3 | 5 | 0.5 | 0.9 | 7.8 | 7.7 |
| **Forests** | 30.5 | 33.1 | 8.3 | 7.2 | 17.6 | 18 | **12** | **13.3** | 1.2 | 0.6 | 26.1 | 25.6 | 15.9 | 14.4 | 23.9 | 23.9 |
| **Pastures** | 0 | 0 | 5.3 | 5.6 | 4.7 | 4.3 | **2.8** | **2.8** | 2 | 2.7 | 2.2 | 2.5 | 1.4 | 1.1 | 2.6 | 2.8 |
| **Rocky areas** | 0.1 | 0 | 1.9 | 1.8 | 4.4 | 4.4 | **2.8** | **2.6** | 3.8 | 5.9 | 2.7 | 2.7 | 1.8 | 2.2 | 7.7 | 5.8 |
| **Shrublands** | 2.2 | 2.5 | 8.5 | 8.7 | 4.6 | 4.6 | **0.9** | **0.2** | 7.9 | 7.6 | 0.8 | 1 | 9 | 9.9 | 6.6 | 6.6 |
| **Settlements** | 0 | 0 | 0.5 | 0.5 | 1.1 | 1.3 | **0.5** | **0.5** | 0 | 0 | 0.3 | 0.4 | 0 | 0 | 0 | 0 |
| **Slope** | 59.8 | 56.9 | 65.3 | 68.1 | 55.2 | 56.4 | **52.5** | **58.5** | 73.1 | 73.7 | 56.5 | 57.6 | 60.6 | 62.7 | 38.2 | 38.4 |
| **AUC** | 0.780 | 0.782 | 0.793 | 0.787 | 0.768 | 0.773 | **0.780** | **0.782** | 0.723 | 0.728 | 0.810 | 0.812 | 0.756 | 0.754 | 0.757 | 0.752 |

**Supplementary Table S6.** Percentage of the number of cells crossed by a road with more than a 70 % probability of bear occurrence (cloglog value > 0.7), and thus, a high habitat suitability, for each bear classes in each season. fcmat = females with cubs during mating; fchyp = females with cubs during hyperphagia; fcden = female with cubs during denning; fymat = females with yearlings during mating; fyden = females with yearlings during denning; omat = other bears during mating; ohyp = other bears during hyperphagia; oden = other bears during denning.

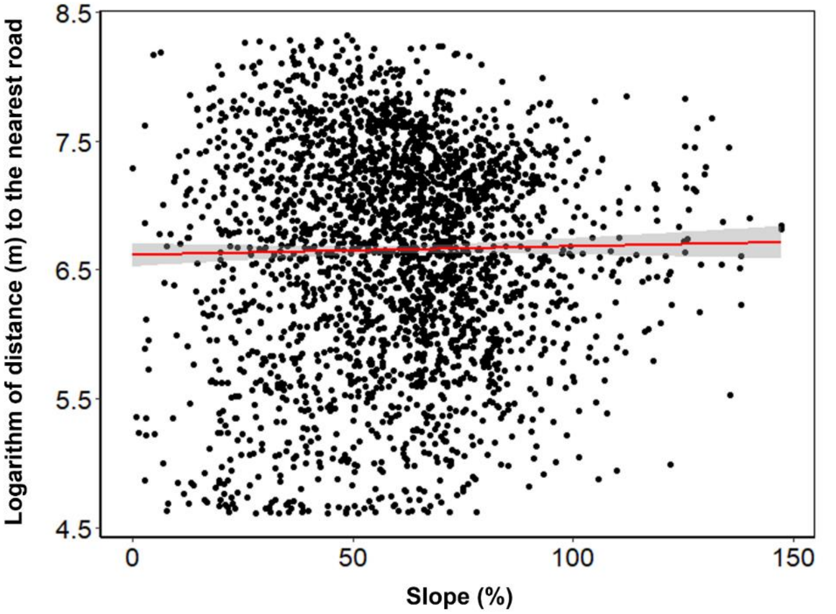
| ***Type of road*** | **fcden** | | **fcmat** | | **fchyp** | | **fyden** | | **fymat** | | **oden** | | **omat** | | **ohyp** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** | **r** | **nr** |
| **1: low traffic** | 11.33 | 10.99 | 8.40 | 7.52 | 8.83 | 8.57 | 9.32 | 8.34 | 14.02 | 12.83 | 6.38 | 6.31 | 8.39 | 7.53 | 5.53 | 5.69 |
| **2: medium traffic** | 13.04 | 12.94 | 11.91 | 10.63 | 11.29 | 11.50 | 12.27 | 10.93 | 16.43 | 15.20 | 8.06 | 8.37 | 10.57 | 9.65 | 7.75 | 7.85 |
| **3: high traffic** | 7.17 | 6.77 | 5.41 | 4.44 | 6.17 | 6.24 | 6.17 | 5.00 | 8.85 | 7.12 | 4.78 | 4.65 | 6.66 | 5.37 | 5.10 | 5.00 |
| **All roads** | 10.24 | 9.83 | 8.07 | 6.93 | 8.47 | 8.39 | 8.99 | 7.69 | 13.06 | 11.37 | 6.38 | 6.41 | 8.85 | 7.69 | 6.42 | 6.45 |
| **% contribution distance to NR** | 0.2 | - | 1.5 | - | 0.4 | - | 13.4 | - | 3 | - | 0 | - | 0.8 | - | 0 | - |

**Supplementary Figures S3.1-3.8.** Effect on the distance of the bear locations to the nearest road of the different variables included in the linear models. The logarithm of the distance to the nearest road is represented instead of the distance itself, in the same way that the models were built.

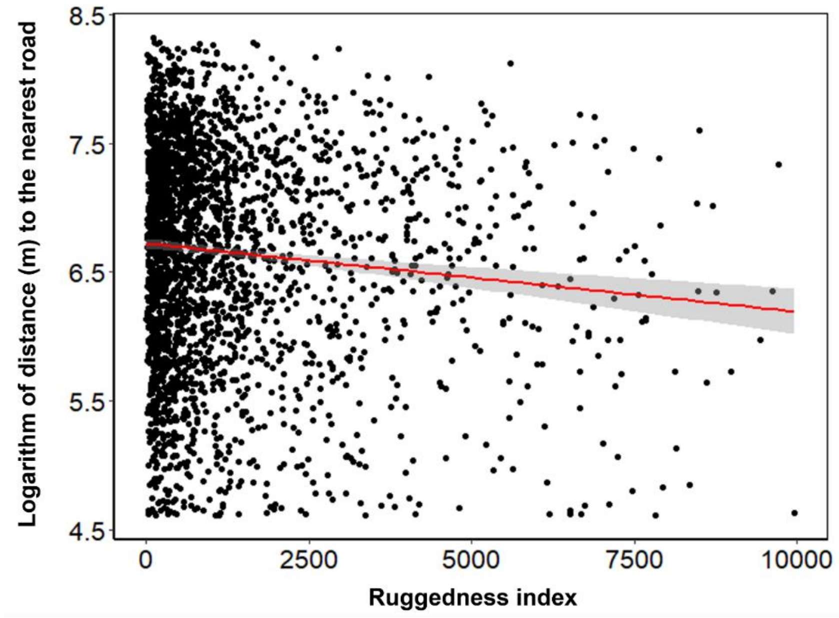
**Supplementary Figure S1.1.** Effect of altitude above the sea level on distance of the bear locations to the nearest road.



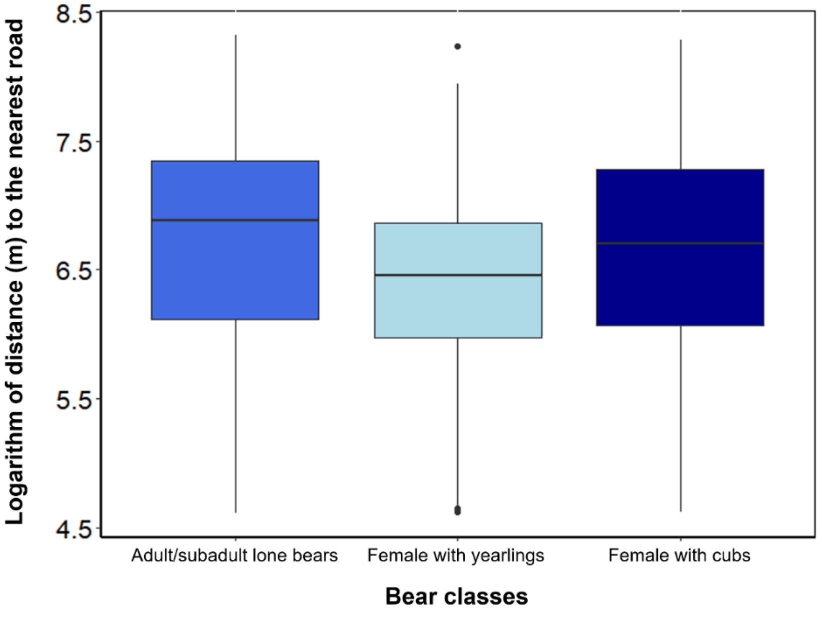
**Supplementary Figure S1.2.** Effect of terrain slope (%) on distance of the bear locations to the nearest road.



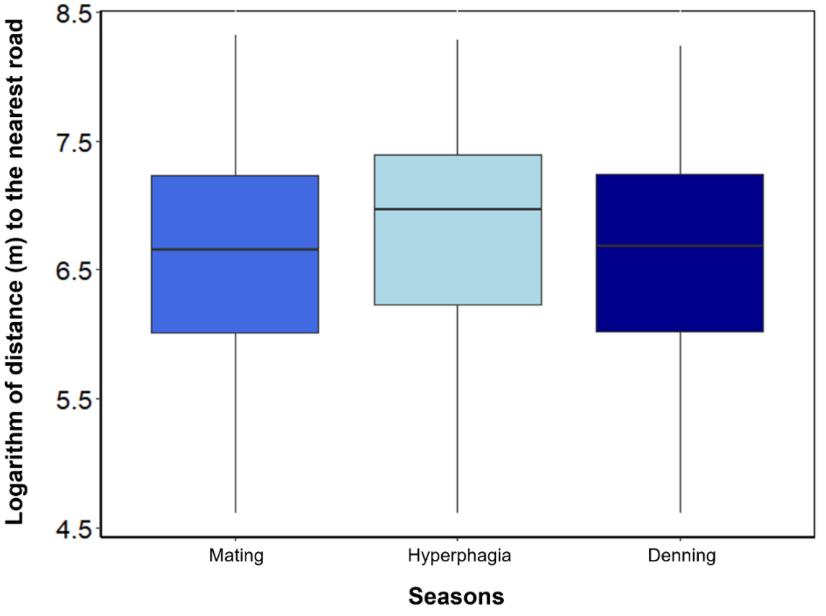
**Supplementary Figure S1.3.** Effect of ruggedness index on distance of the bear locations to the nearest road.



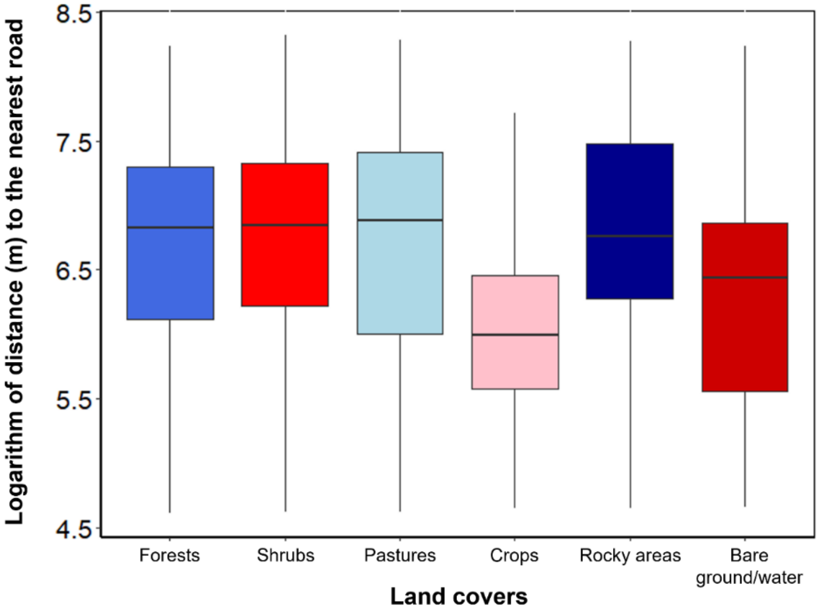
**Supplementary Figure S1.4.** Distance of the bear locations to the nearest road of the three classes of bear considered.



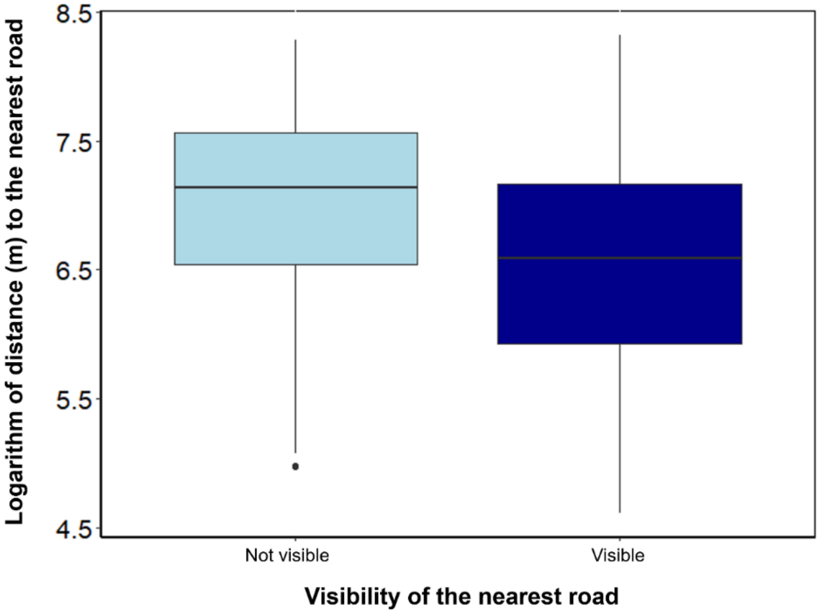
**Supplementary Figure S1.5.** Distance of the bear locations to the nearest road depending on the season.



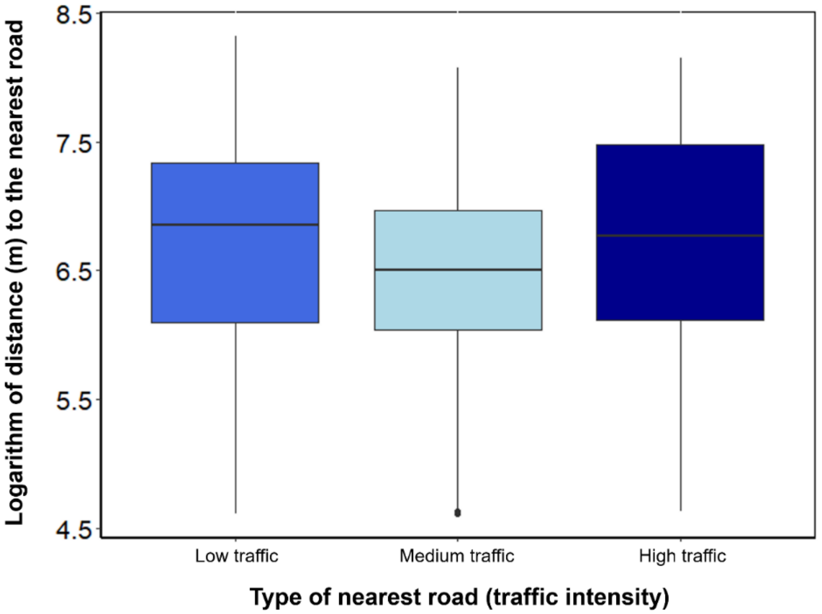
**Supplementary Figure S1.6.** Distance of the bear locations to the nearest road at the different land covers considered.



**Supplementary Figure S1.7.** Distance of the bear locations to the nearest road based on the visibility of the nearest road.

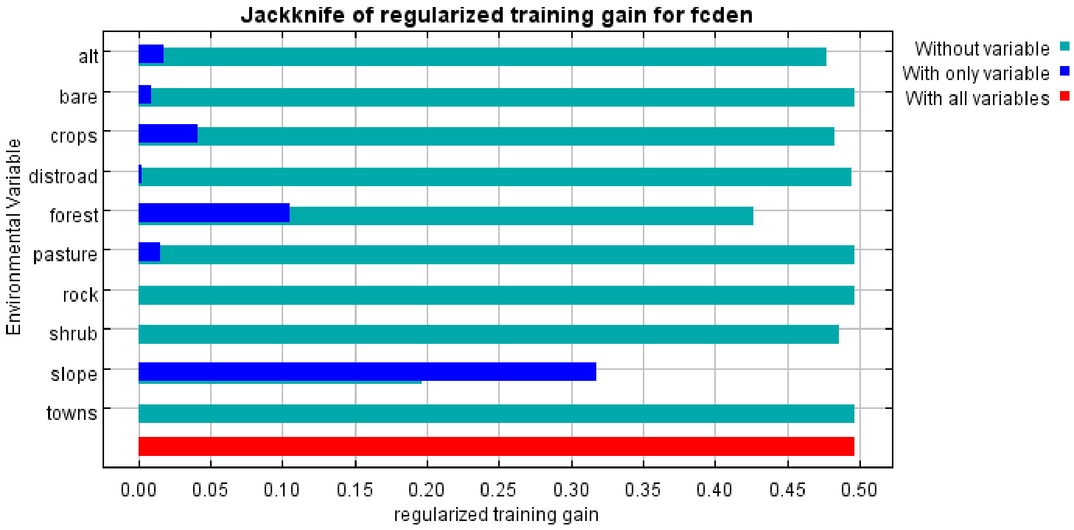


**Supplementary Figure S1.8.** Distance of the bear locations to the nearest road depending on the type (traffic intensity) of the nearest road. Traffic intensity: “low traffic” = 0-337 vehicles per day; “medium traffic” = 338-1411 v/d; “high traffic” = 1412-5129 v/d.

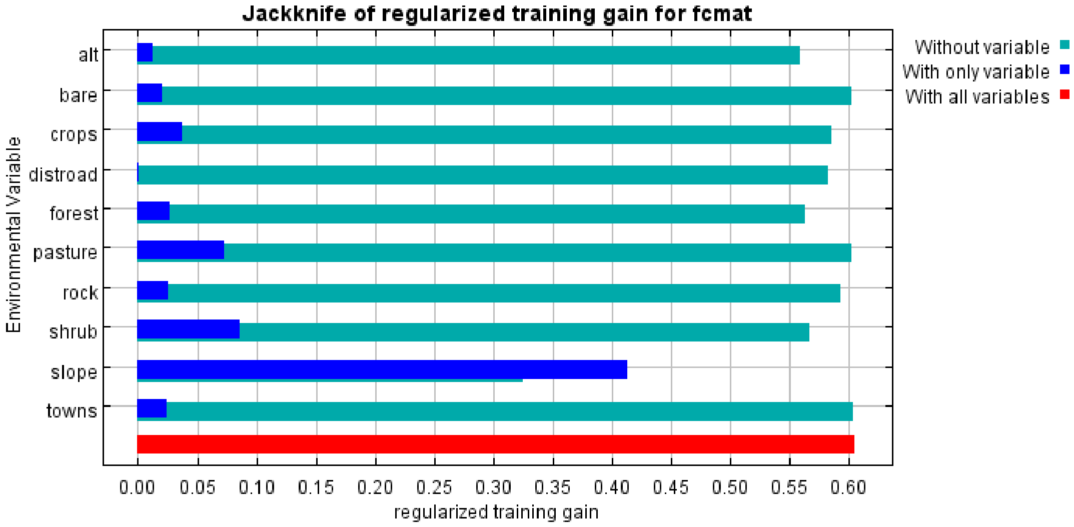


**Supplementary Figure S2.1-2.8.** Jackknife tests of variable importance for regularized training gain. The environmental variable with highest gain (biggest dark blue bar) when used in isolation has the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted (smallest light blue bar) has the most information that isn't present in the other variables.

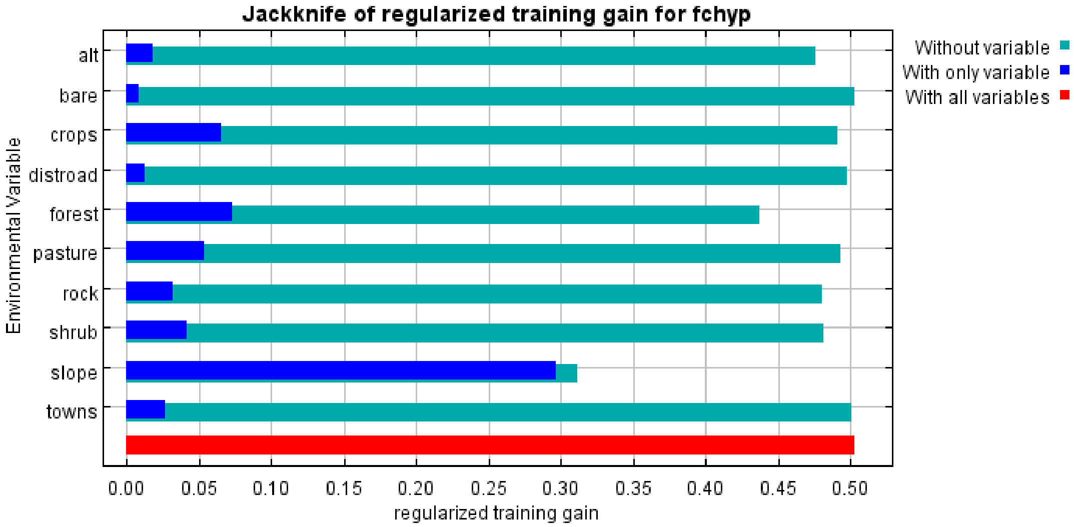
**Supplementary Figure S2.1.** Jackknife tests of variable importance for regularized training gain of the model for females with cubs during the denning season (fcden).



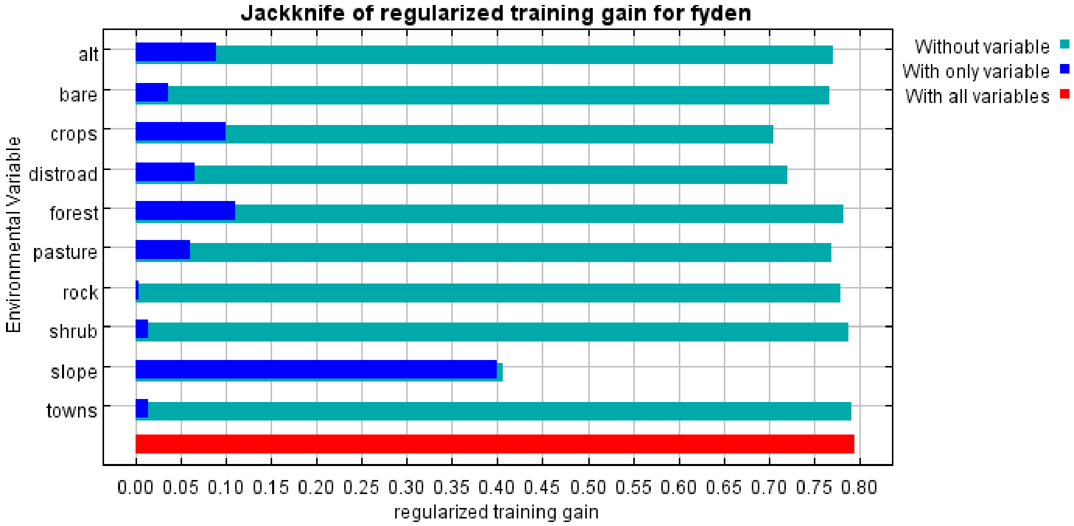
**Supplementary Figure S2.2.** Jackknife tests of variable importance for regularized training gain of the model for females with cubs during the mating season (fcmat).



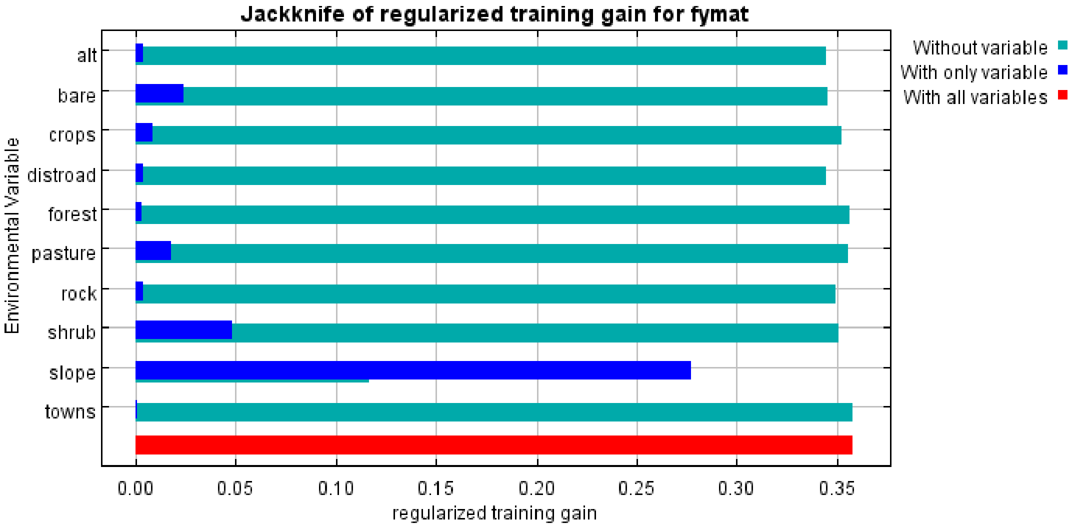
**Supplementary Figure S2.3.** Jackknife tests of variable importance for regularized training gain of the model for females with cubs during the mating season (fchyp).



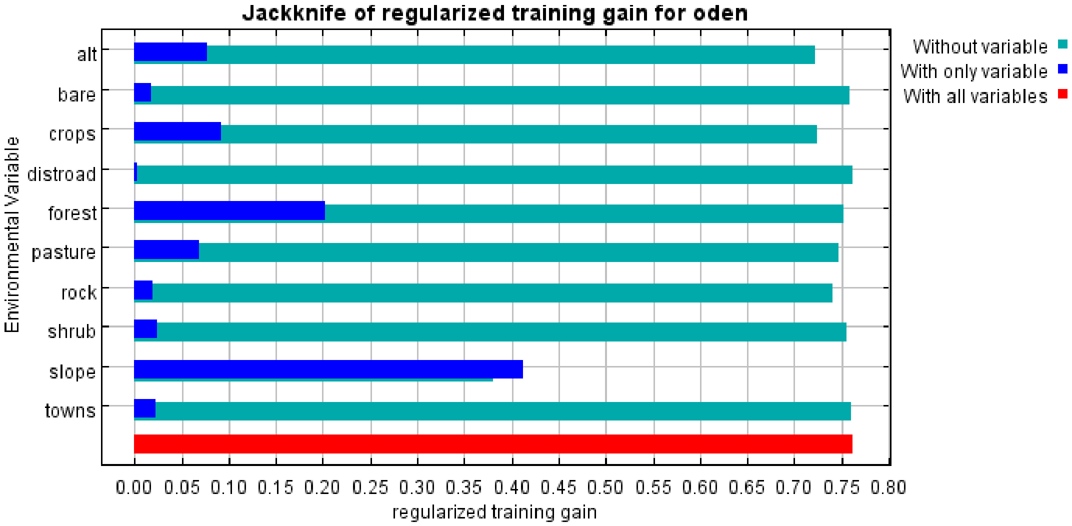
**Supplementary Figure S2.4.** Jackknife tests of variable importance for regularized training gain of the model for females with yearlings during the denning season (fyden).



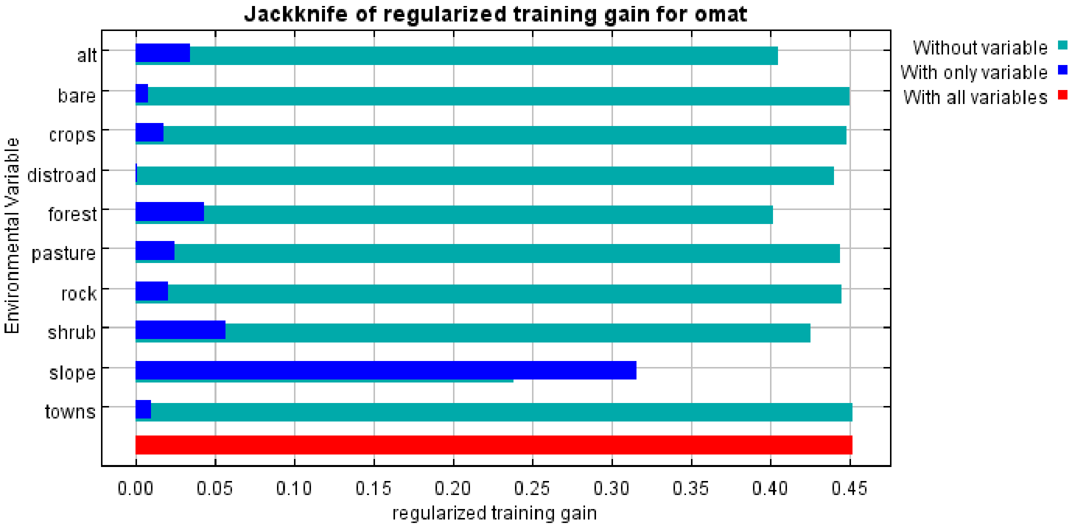
**Supplementary Figure S2.5.** Jackknife tests of variable importance for regularized training gain of the model for females with yearlings during the mating season (fymat).



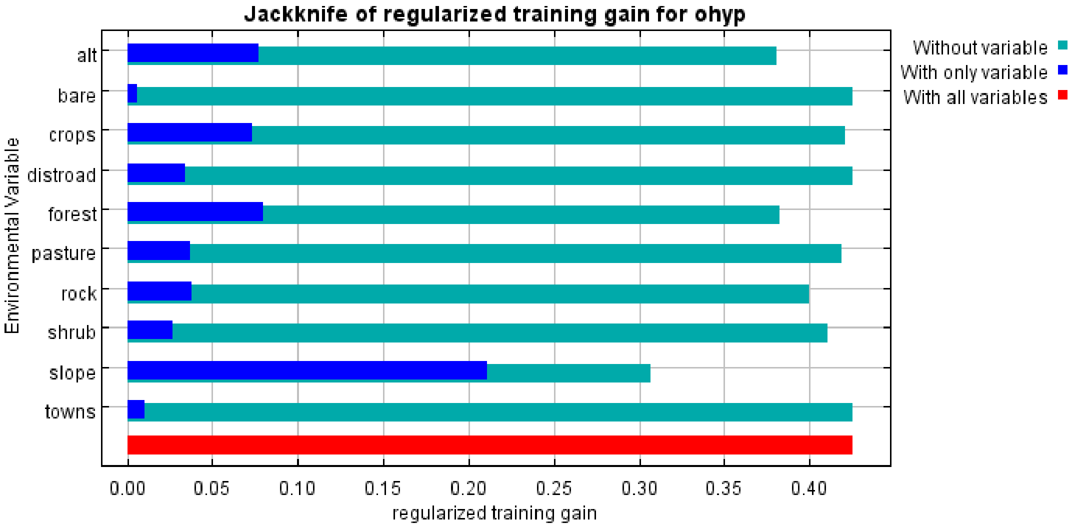
**Supplementary Figure S2.6.** Jackknife tests of variable importance for regularized training gain of the model for lone adults/subadults during the denning season (oden).



**Supplementary Figure S2.7.** Jackknife tests of variable importance for regularized training gain of the model for lone adults/subadults during the mating season (omat).

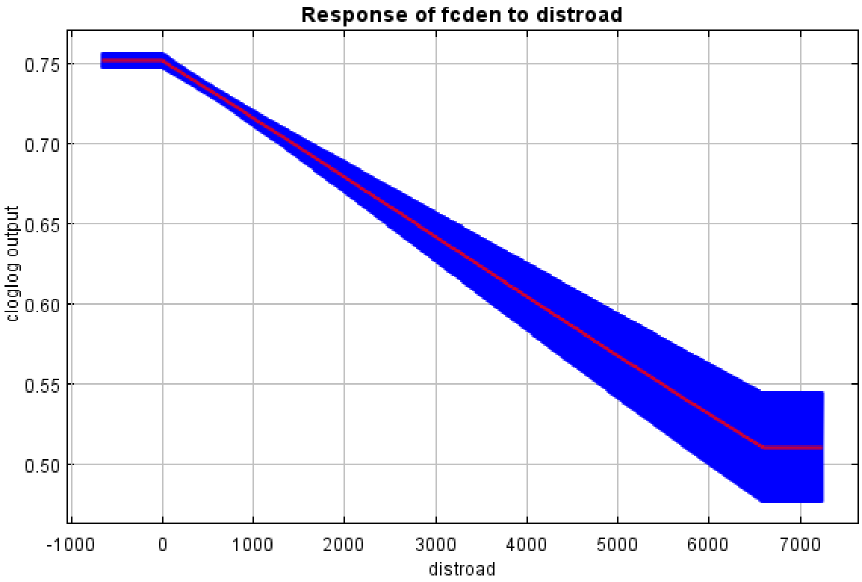


**Supplementary Figure S2.8.** Jackknife tests of variable importance for regularized training gain of the model for lone adults/subadults during the hyperphagia season (ohyp).

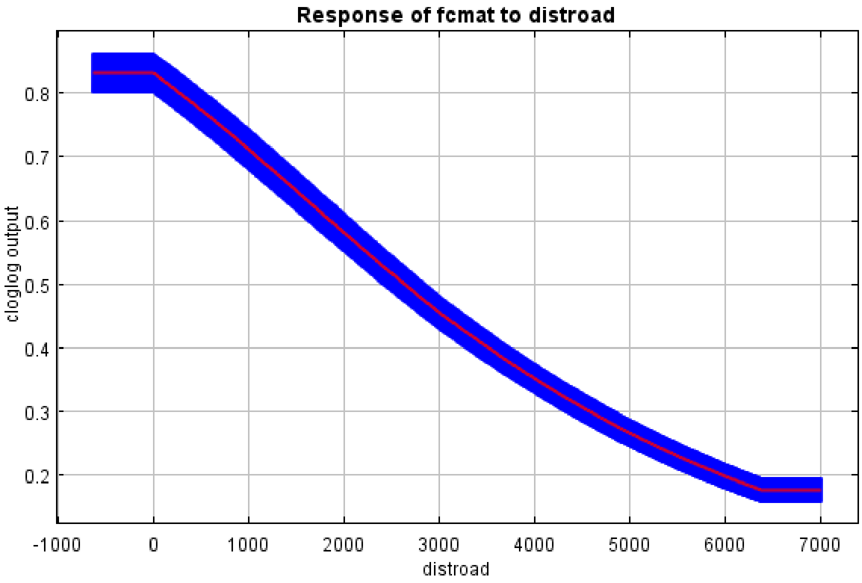


**Supplementary Figures S3.1-3.8.** Response curves of the relationship between bear occurrence probability and the variable distance to NR**.** The curves show how the predicted probability of presence changes as each environmental variable is varied, keeping all other environmental variables at their average sample value.

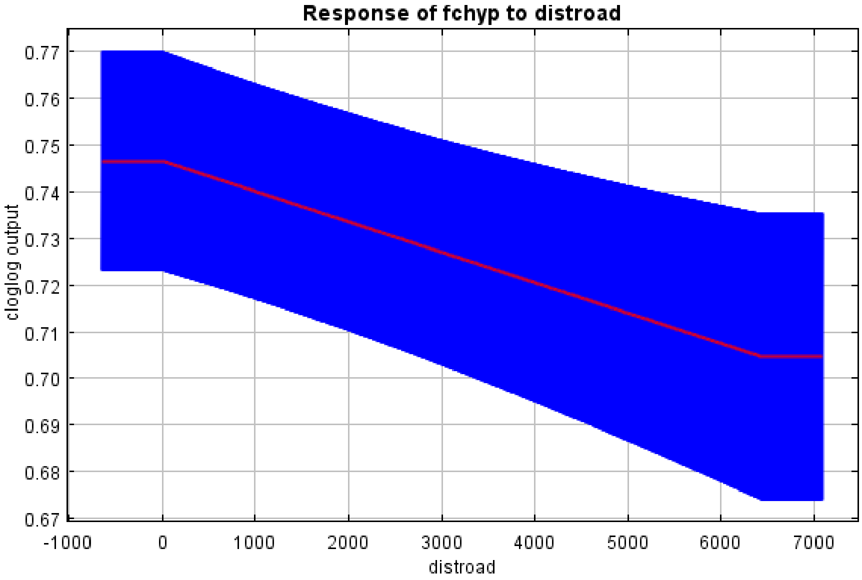
**Supplementary Figure S3.1.** Response curve of the relationship between bear occurrence probability and the variable distance to NR of the model for females with cubs during the denning season (fcden).



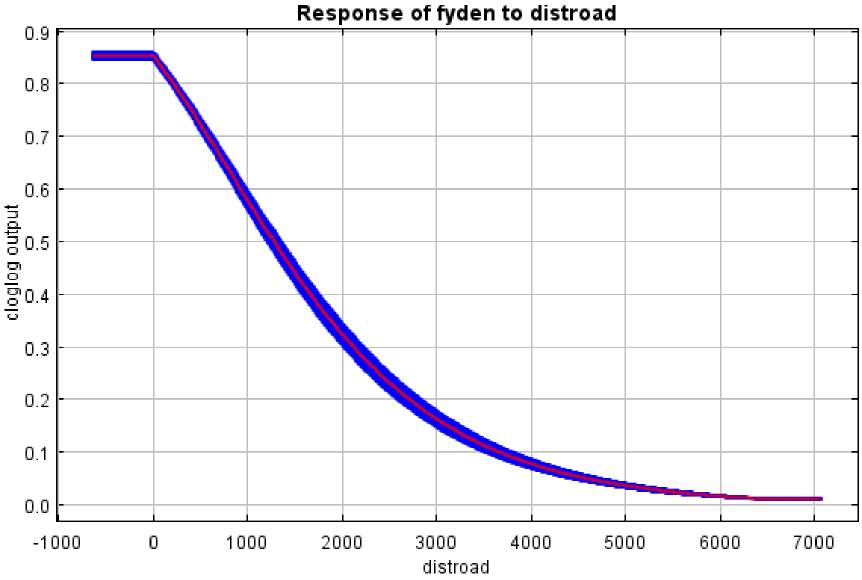
**Supplementary Figure S3.2.** Response curve of the relationship between bear occurrence probability and the variable distance to NR of the model for females with cubs during the mating season (fcmat).



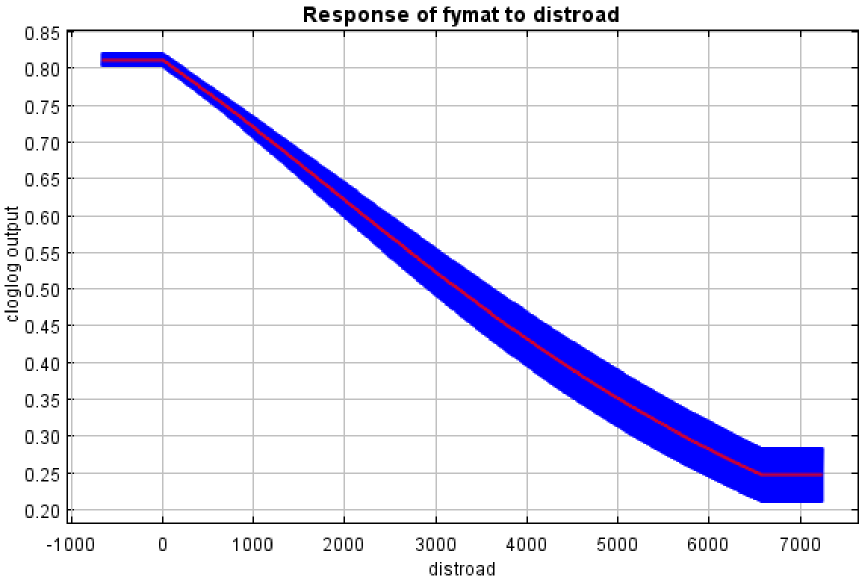
**Supplementary Figure S3.3.** Response curve of the relationship between bear occurrence probability and the variable distance to NR of the model for females with cubs during the hyperphagia season (fchyp).



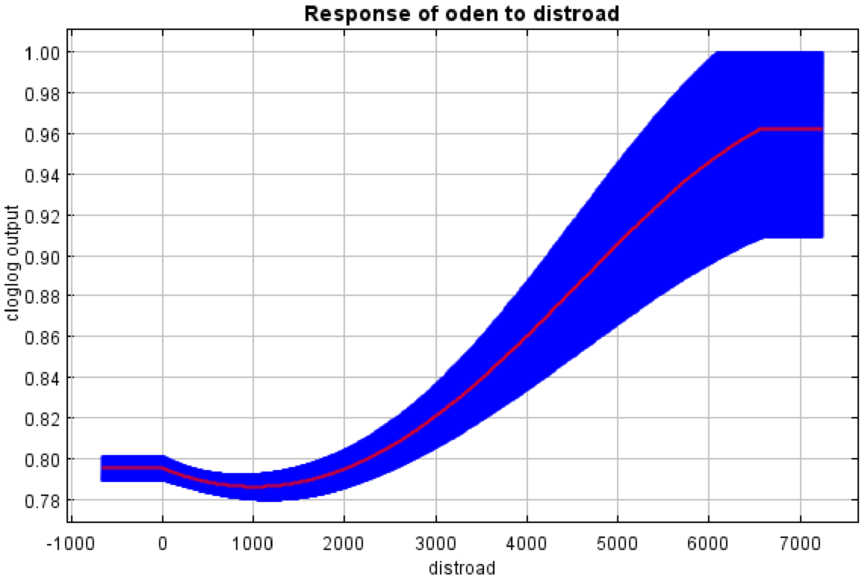
**Supplementary Figure S3.4.** Response curve of the relationship between bear occurrence probability and the variable distance to NR of the model for females with yearlings during the denning season (fyden).



**Supplementary Figure S3.5.** Response curve of the relationship between bear occurrence probability and the variable distance to NR of the model for females with yearlings during the mating season (fymat).

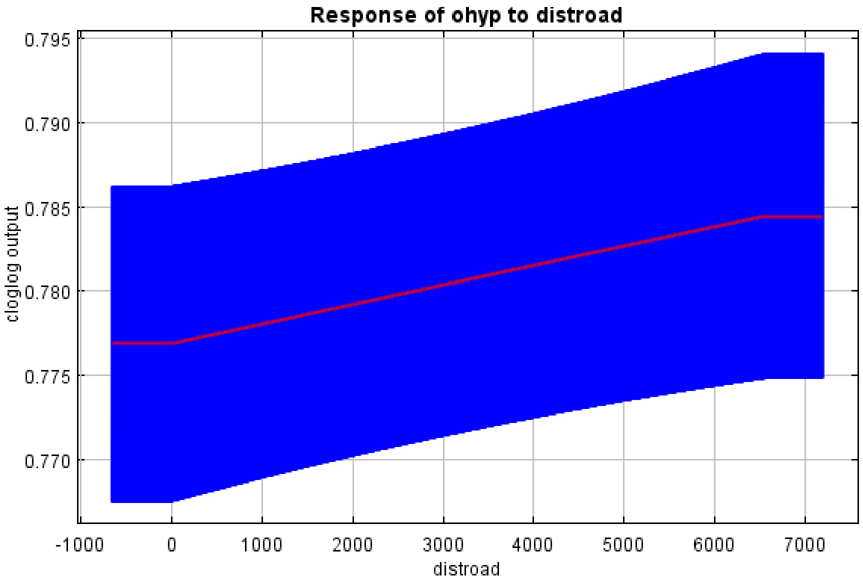


**Supplementary Figure S3.6.** Response curve of the relationship between bear occurrence probability and the variable distance to NR of the model lone adults/subadults during the denning season (oden).



**Supplementary Figure S3.7.** Response curve of the relationship between bear occurrence probability and the variable distance to NR of the model lone adults/subadults during the mating season (omat).

**Supplementary Figure S3.8.** Response curve of the relationship between bear occurrence probability and the variable distance to NR of the model lone adults/subadults during the hyperphagia season (ohyp).



# General Discussion

The main objective of my doctoral thesis has been to generate new scientific knowledge on the behaviour and ecology of Cantabrian brown bears. This objective has been fulfilled, with five chapters that contribute to fill previous information gaps and facilitate and promote more research in these fields.

Firstly, chapters I and II have dealt with a critical period in the life cycle of the species, the hibernation. The results presented in the first chapter suggest that both ultimate and proximate factors determine the triggering of hibernation and the associated physiological processes that make hibernation such an effective mechanism (Carey et al. 2003). First, my review highlights the enormous plasticity of bears, which can modify the chronology of hibernation under the very changing climatic conditions that they experience in their huge distribution range, as also described in other ursids (Fowler et al. 2019). Some adaptations to climatic changes have also been reported in other species, which show certain resilience and develop adaptive responses through microevolutionary processes or phenological plasticity (Dawson 2011; Karell et al. 2011; Bellard et al. 2012; Radchuk et al. 2019), with examples in a multitude of plant and animal taxa (Kovach et al. 2012; Thompson et al. 2013; Palumbi et al. 2014; Bonamour et al. 2019). However, the real effect and magnitude of these fluctuations are still largely unknown (Hertel et al. 2018), which demands more applied research to discern the potential effects that climate changes have on individual fitness and the viability of brown bear populations. Even more so considering that the effects of climate change are exacerbated in those species or populations that inhabit highly anthropized environments, such as many populations of brown bears (Fahrig 2007; Pimm et al. 2014). Second, it is worth noting the impact that human activities may have on the hibernation period of the brown bear (Linnell et al. 2000; Evans et al. 2012). In particular, the availability of anthropogenic food, especially supplementary feeding for hunting purposes, may shorten the hibernation period, which has the potential to exacerbate conflicts with humans, as bears are active in a period where otherwise they would not be (Penteriani et al. 2017, 2018), and ultimately condition the survival of individuals (Lamb et al. 2017b; Bombieri et al. 2018; Zarzo-Arias et al. 2018). Finally, some knowledge gaps regarding hibernation have also been evidenced in this review.

In line with the previous one, the environmental and individual conditioning factors that determined the end of the hibernation period of a specific class of bears, i.e., females with cubs, have been investigated in the second chapter. Pregnant females are the only bears showing obligated hibernation at our latitudes. An inverse relationship was found between the maximum temperatures in the month prior to the emergence of the winter den and the den emergence, similar to that found in other similar populations (Miller 1990; Mcloughlin et al. 2002; Manchi and Swenson 2005; Delgado et al. 2018). In addition, a positive relationship has been detected between latitude and hibernation length, which seems to be related with the less adverse climatic conditions at lower latitudes (Manchi and Swenson 2005; Fowler et al. 2019). From the results obtained in the first two chapters, it becomes clear that understanding these determinants of hibernation is crucial in the current context of climate change. Elements such as the expected rise of several degrees during this century (IPCC 2013; Raftery et al. 2017) and the increase in variability and extreme nature of atmospheric phenomena (Giorgi et al. 2004; Pendergrass et al. 2017) may have an effect on phenological or climate-dependent biological mechanisms, such as hibernation, as already demonstrated for other organisms (Root et al. 2003; Turbill and Prior 2016). As climate change modifies the distribution and abundance of wild plants and animals (Root et al. 2003; Parmesan 2006), reductions in the abundance of trophic resources and / or change their availability have been predicted in our study area (Rodríguez et al. 2007; Monzón et al. 2011; Penteriani et al. 2019). This, regarding the phenology of hibernation bears, has the potential to create mismatches (Holden et al. 2012; Deacy et al. 2017) that through different mechanisms such as a decrease in physical condition or an increase in offspring mortality, can reduce the viability of brown bear populations (Pigeon et al. 2016a; Albrecht et al. 2017; Delgado et al. 2018; Hertel et al. 2018). Likewise, fluctuating chronologies can force bears to search for food of human origin and thus increase bear-human conflicts and mortality (Penteriani et al. 2019; Zarzo-Arias et al. 2020). Moreover, effects of climate changes would particularly affect populations located at the limit of the distribution range and located in mountainous environments, such as southwestern Europe (Root et al. 2003; Brunetti et al. 2009; Penteriani et al. 2019). This fact, together with the isolated and humanized habitat in which the Cantabrian population of brown bears inhabit, makes it particularly vulnerable (Fahrig 2007; Pimm et al. 2014). For this reason, it seems to me of vital importance, on the one hand, to deepen the knowledge and monitoring of the possible effects of climate change on this population or other similar ones, and on the other hand, to consider it as an ideal candidate to develop and test prevention and mitigation measures of these impacts.

Marking behaviours of brown bears have also received my attention over the thesis, as intraspecific communication in this species is a little-studied and highly interesting aspect. First (chapter III), I have analysed characteristics of rubbing trees, as well as the intrinsic factors of the population that may determine the abundance of rubbing trees in a given area. In this study, as in others carried out in other populations, these trees were mostly found along the paths and routes frequented by bears, which very frequently are trails and paths (Nie et al. 2012; Clapham et al. 2013) that bears use to travel (Seryodkin et al. 2014; Tattoni et al. 2015). Secondly, rubbing trees were characterised by their conspicuousness, which may increase their function as chemical signal in intraspecific communication. Indeed, bears preferred larger trunk diameters and as well as a greater distance to surrounding trees, as also reported in other populations of the Northern Hemisphere (e.g., Puchkovskiy et al. 2012,Clapham et al. 2013,Sato et al. 2014). A greater space available for marking would facilitate the realization of the visual marks and the deposition of the chemical signals (Seryodkin et al. 2014). Additionally, a preference towards certain species for marking was detected, conifers and birches being marked in a greater proportion to their availability. The use of conifers for rubbing has been described in other populations that inhabit coniferous or mixed forests. This has been suggested to be due to the aromas produced by these species that could increase or lengthen the chemical signal deposited by bears (Puchkovskiy 2009; Nie et al. 2012; Clapham et al. 2013; Sato et al. 2014). In this study, carried out in an area dominated by temperate forest where conifers only appear as part of forest plantations, their use seems to be due to a positive selection by bears. The other positively selected species, the birch, does not seem related to its chemical characteristics, if not for the ease of laceration and colour of its bark, which makes the marks made by bears more attractive for marking. The observation of this fact in birch trees led me to think that these marks have a function in themselves, and that this could be the transmission of visual information, which would be favoured by contrast in low visibility situations, as has been done reported in other species (Penteriani and Delgado 2017). Starting from this idea, the study collected in the fourth chapter was developed. On the other hand, I did not detect any effect of the density of bears in the rubbing tree linear abundance, nor did it detect any effect due to its position within the population distribution range. The individual characteristics of these rubbing trees and their position spread throughout the territory occupied by bears give an idea of their importance in intraspecific communication. These trees, frequently used for several generations of brown bears (Clapham et al. 2013; Morgan Henderson et al. 2015), can represent a crucial tool for monitoring bear populations or specific individuals (e. g. dispersing or reproductive individuals) or conduct censuses through biological samples or camera traps as well as core areas of communication. For this reason, I suggest that the conservation of these trees should be a priority, both because of their importance for the species and because of their usefulness in their management and conservation.

Following, in the fourth chapter, I have explored the possible visual function of the marks left by the brown bear on trees. The chemical marking in brown bear trees is carried out through the glandular secretions (Sergiel et al. 2017; Tomiyasu et al. 2017) and is associated with the transmission of information about the reproductive status and communication of dominance in males (Clapham et al. 2012; Tattoni et al. 2015; Lamb et al. 2017a). However, visual signalling in mammals has been little studied in general, since olfactory communication is considered dominant in this animal group (Warrant 2004; Penteriani and Delgado 2017). Based on: (1) the results of the third chapter, (2) the evident role that colouration has in mammal communication (Caro et al. 2017; Moreira et al. 2019) and (3) the potential advantages of visual communication (persistence and remote functioning, Penteriani and Delgado 2017), an experiment was developed with the aim of exploring the possibility that a new and overlooked form of visual communication might exist in mammals. This visual signalling behaviour is based on conspicuous marks produced by trees debarking by biting or scratching. This behaviour also seems deeply related to reproductive functions, being fundamentally carried out by males during the mating season, and probably linked to the communication of the physical condition (e.g., male size) of individuals. The demonstration of the existence of this behaviour is a first step in the investigation of visual communication pathways in mammals, particularly in carnivores. Understanding wildlife behaviour, in this case intraspecific communication, is a powerful conservation and management tool (Greggor et al. 2019). Thus, in line with what was stated for the previous chapter, the identification and monitoring of those rubbing trees where visual marking is performed can provide very useful and specific information on certain individuals such as reproductive adult males. Furthermore, its predominantly seasonal use can facilitate selective monitoring of mating areas and movements of breeding individuals. In addition, they constitute a centre of activity within the area inhabited by brown bears, and whose targeting as monitoring hotspot is particularly interesting in the mating season because it concentrates a large number of visits from different individuals.

Finally, in the last chapter, I have taken into account the direct and indirect factors that may influence the impact that local road network on brown bear distribution. Results highlighted little effect of topographic, bear population, or human activity factors. As a conclusion, roads seem to produce a moderate effect on bear locations, which, like other species that live in anthropized environments, have managed to adapt to anthropic pressures by modifying their behaviour (Ciuti et al. 2012; Johann et al. 2020; Srivastava et al. 2021). Adaptation patterns have been described in different brown bear populations (Ordiz et al. 2011, 2012; Zarzo-Arias et al. 2018; Lamb et al. 2020) as well as in other species of large carnivores, allowing a certain degree of coexistence with humans in human-modified landscapes (Fuller and Sievert 2001; Støen et al. 2015; Carter and Linnell 2016). Large carnivores have sometimes been considered particularly vulnerable to human pressure, as they are long-lived species with low reproductive potential, low population density, and high space requirements (Fahrig and Rytwinski 2009; Hetem et al. 2014). However, the previously described adaptations suggest a certain degree of tolerance and adaptation of these species to human activities and infrastructures, which appear more resilient than they have sometimes been considered. However, given the limitations of our approach (indirect and correlative analyses only), potential negative effects of roads on e.g., bear mortality or movement patterns should not be discarded, considering that road networks have revealed their potential as ecological traps in telemetry studies, since they can be attractive due to accessible food resources or for facilitating movement (Penteriani et al. 2018, Morales-González et al. 2020). The results obtained in this chapter, compared to similar studies carried out in different areas of the brown bear's range, confirm the behavioural differences towards roads between European and North American populations. As a general pattern, fewer impacts and greater habituation and tolerance have been described in European populations, which would be the consequence of millennia of coexistence and persecution as opposed to the much more recent occupation of North America and the more intense and effective persecution of its populations (Morales-González et al. 2020; Støen et al. 2020). These differences would have motivated different behavioural and physiological responses and even evolutionary selection such as greater tolerance to human presence and less conspicuous and aggressive behaviours in Europe (Ordiz et al. 2014; Benazzo et al. 2017; Zarzo-Arias et al. 2018). This set adaptations resulting from the continuous presence of the human being in the bear ranges (Colangelo et al. 2012; de Gabriel Hernando et al. 2020) makes populations such as the Cantabrian brown bear unique. I suggest that it is crucial to consider these different responses between populations to human pressures the specific characteristics of each population when designing management and conservation measures for brown bears and, more generally, large carnivores. In this way, the maximum effectiveness of these measures would be achieved, not only with a direct benefit for the species but would also result in greater resource efficiency in management and conservation plans, and ultimately in a better coexistence between humans and large carnivores.

As a conclusion to this general discussion, I want to highlight the transversal nature of the scientific knowledge generated in this doctoral thesis to understand the ecology and behaviour of large carnivores in human-modified landscapes. Although the brown bear has been used as a biological model, and more specifically a population with certain peculiarities such as the Cantabrian population, the results and applications presented here are potentially expandable to other species. Especially to large carnivores, not only because they share similar biological characteristics (Fahrig and Rytwinski 2009), but also because they suffer in a similar way from human persecution and the impacts of their activities, which in many cases have led to local extirpation (Bombieri et al. 2018; Lamb et al. 2020). In addition, the studies carried out within the framework of this thesis, together with the previously published literature, show particular behavioural and ecological singularities of the populations of large carnivores when they inhabit environments with high human intervention. Although these territories are not usually considered optimal for these species (Støen et al. 2015; López-Bao et al. 2017), in many cases they represent a large part of the potential distribution range of these species and their conservation must be focused on them (Di Minin et al. 2016; Milanesi et al. 2017). The survival or recovery of populations of large carnivores in some of these areas proofs their potential for coexistence with humans (Zarzo-Arias et al. 2018) and their deep integration as part of these territories (Mace 2014; Carter and Linnell 2016). Therefore, if we want to ensure their conservation, in addition to considering them a fundamental part of our environment, it is essential to know how they behave or what ecological characteristics species such as the brown bear have when they live in human-modified landscapes or suffer human pressure. This is what has been achieved in this thesis for the case studied, a small population of brown bear, isolated and living on the periphery of the range of distribution of the species. On one side, their special vulnerability to the effects of climate change has been highlighted, particularly in a period strongly dependent on climatic conditions such as hibernation. This vulnerability contrasts with the apparent adaptation and habituation of these brown bears to human activities and infrastructures such as vehicle traffic and roads. On the other hand, certain features of intraspecific communication of the spice have been assessed, yielding novel and highly applicable conclusions. I hope that the new scientific knowledge generated in this thesis will promote specific research based on populations characteristics, in addition to encourage the development of adapted management and monitoring tools, with the ultimate goal of promoting human-bear coexistence and ultimately the conservation of the species.

# Conclusions

1.- Human impact on human-modified landscapes has diverse consequences on ecosystems, and has often forced the species to adapt to these pressures. This is particularly relevant in the case of large carnivores, which are especially vulnerable due to their biological characteristics and the historical persecution to which they have been subjected. A deeper understanding of the behaviour and ecology of these species in these environments is crucial for the proper conservation and management of their populations.

2.- Hibernation is a critical period in the life of brown bears, allowing them to overcome unfavourable periods. The chronology of hibernation, which varies by sex and age classes, is a function of both environmental and geographical variables, and there is a latitudinal gradient in hibernation. The choice of a winter den is based on the selection of certain fine and coarse scale habitat characteristics, and the physical condition or survival of individuals may depend on it.

3.- Hibernation in brown bears is a metabolic challenge in which several unique physiological adaptations have evolved. These allow them to withstand extreme situations such as food or water deprivation, the absence of excretion and high levels of lipids and nitrogen compounds in the body, as well as preventing cardiovascular pathologies and the deterioration of their muscular and skeletal systems.

4.- With regard to hibernation, it is important to distinguish between proximate factors (environmental conditions) and ultimate factors (biological processes shaped in the course of evolution), as well as to differentiate properly between the actual drivers of hibernation and its correlates. On the other hand, hyperphagia and prehibernation periods of the species, closely related to hibernation and on which its success depends, need to be better understood.

5.- The timing of the end of hibernation of females with cubs in the Cantabrian Mountains depends on the maximum temperature in the previous days. Here, the hibernation chronology varies annually and is consequent with the latitudinal gradient existing between different brown bear populations, which proves the plasticity exhibited by the species and its capacity for adaptation.

6.- Given the effect of temperatures on the timing of hibernation, it is essential to understand and investigate the possible effects of Global Change on brown bears, such as potential mismatches between the hibernation chronology and food availability, which may have effects on the physical condition of individuals and an increase in conflicts with humans. This is particularly relevant where these environmental changes are expected to have the greatest impact, such as in the Cantabrian Mountains.

7.- Chemical communication based on the deposition of scents on marking trees is the main means of intraspecific communication in brown bears. The selection of these trees is based on individual and environmental characteristics, which increase the conspicuousness of the signal and the ease of deposition and reception of the information, rather than to population variables or geographical location within the range of the species.

8.- Visual communication has been overlooked in many animal groups, including mammals. However, species such as the brown bear through markings on trees bark, employ it for intraspecific communication. This communication channel seems to have a more restricted use than chemical marking, being related to dominance communication between males during the mating season of the species.

9.- The use of marking trees (chemical and visual) as communication nodes in bear populations can be a valuable tool for monitoring and managing the species. Population censuses or the tracking of specific individuals through these locations would allow for more efficient and complete data collection and therefore generate higher quality information with less effort.

10.- Roads and the traffic have a profound impact on ecosystems and species, including the brown bear. Despite this, in those populations which have inhabited a antrophized environment for millennia, such as the Cantabrian region, bears seem to show a certain habituation and tolerance to human presence and its infrastructures and activities. These adaptations seem to be less present in populations that occupy environments with little or recent human presence.

11.- In order to achieve appropriate conservation and management of large carnivore populations, and hence coexistence with humans, the particularities of each population, especially those that inhabit human-modified landscapes, need to be taken into account. These particularities of their behaviour and ecology, and their response and adaptation to human pressures, depend on historical exposure to humans and their activities.

# Resumen y Conclusiones

## Introducción general

Los paisajes humanizados son entornos que pueden definirse como aquellos ambientes con amplia presencia de seres humanos, de sus actividades y de sus infraestructuras. En ellos, el ser humano ha alterado profundamente los hábitats modificando su estructura, funciones, biodiversidad, etc. Las especies que habitan en ellos han conseguido adaptarse en mayor o menor medida a las presiones antrópicas, modificando su comportamiento, fisiología y uso del espacio. Sin embargo, estas adaptaciones pueden tener costes en la reproducción, la condición física o supervivencia de los individuos. Este impacto humano se ha visto exacerbado en las últimas décadas como consecuencia del cambio climático, que altera los hábitats, la distribución de las especies, la disponibilidad de recursos e incrementa las tasas de extinción, lo que es particularmente preocupante en poblaciones aisladas o vulnerables como muchas de las que habitan en entornos humanizados.

Entre las especies más vulnerables a estos efectos se hallan los grandes mamíferos, dadas sus características particulares como grandes requerimientos espaciales y tasas de reproducción bajas. En el caso de los grandes carnívoros, esta vulnerabilidad se ve incrementada por la persecución a la que son sometidos al ser considerados una amenaza para las personas o sus bienes. En muchas partes del planeta sus poblaciones han sido perseguidas hasta la erradicación o han quedado reducidas y relegadas a lugares remotos. Tal es el caso de la mayor parte de Europa, donde los grandes carnívoros cohabitan con el hombre desde hace milenios en espacios fuertemente intervenidos. En las últimas décadas se han recuperado en algunas partes de sus antiguos rangos de distribución, dando muestras de que la coexistencia es posible y de que deben ser considerados una parte más de los ecosistemas.

En el caso concreto del oso pardo, la distribución en Europa está mayoritariamente restringida a áreas boscosas y montañosas, con presencia de actividades humanas diversas. En el sur del continente las poblaciones remanentes de osos pardos han quedado relegadas a zonas montañosas, encontrándose aisladas entre sí. Los individuos de estas poblaciones han desarrollado algunas características comportamentales, fisiológicas e incluso genéticas particulares fruto de la persecución milenaria, como una dieta más vegetariana, un comportamiento menos agresivo y una actividad más nocturna. Tal es el caso de la pequeña, amenazada, y aislada población de oso pardo cantábrico, aislada de otras poblaciones más de 300 km y dividida en dos pequeñas subpoblaciones que suman unos 300-350 individuos. En una población de estas características es importante conocer las particularidades comportamentales y ecológicas que la definen a fin de conservarla y manejarla adecuadamente. Más incluso teniendo en cuenta el papel que realizan los osos pardos en el ecosistema y su papel como especie “paraguas” y “bandera” en los hábitats que ocupa. Con vistas a lo anterior se planteó el objetivo principal de la tesis doctoral: arrojar luz sobre aquellos aspectos aún poco investigados del comportamiento y la ecología de los osos pardos en ambientes humanizados. Con este fin esta tesis se estructura en torno a cinco capítulos:

## Capítulo I. La hibernación en el oso pardo.

Introducción. La hibernación representa una adaptación para superar condiciones ambientales adversas- Es un periodo crítico de la vida de los osos pardos donde, por ejemplo, tiene lugar el parto de las hembras preñadas. El conocimiento detallado de este periodo es crucial para la conservación y el manejo de la especie. En este capítulo se llevó a cabo una revisión bibliográfica de la literatura científica publicada acerca de tres aspectos clave: la cronología de la hibernación, la selección de la hibernación y la fisiología de la hibernación.

Material y métodos. La búsqueda de artículos se llevó a cabo a través de las bases de datos de Google Académico y Scopus, combinando los términos 'bear', 'grizzly' y 'Ursus arctos' con los términos 'den', 'denning chronology', 'denning ecology', 'den entry', 'den exit', 'hibernation', 'hibernation driver' and 'phenology', obteniendo un total de 148 publicaciones. Las variaciones latitudinal y altitudinal de la cronología de la hibernación se testaron a través de correlaciones de Pearson y Spearman, respectivamente.

Resultados.

*Cronología de la hibernación*. Se identificaron varios aspectos clave en cuanto a la cronología de la hibernación. El primero de ellos es la existencia de un periodo de pre-hibernación donde los osos acumulan reservas grasas y comienzan los cambios comportamentales y de actividad necesarios. En cuanto a la hibernación en sí, se describen diferencias por clases de sexo y edad, con las hembras preñadas siendo las primeras en entrar en las oseras y las últimas en salir, debido a los cuidados que los recién nacidos precisan. Los machos adultos y los subadultos presentan el patrón contrario. Estas fechas son variables espacial y temporalmente, y parecen obedecer tanto a condiciones ambientales como a la disponibilidad de alimento. Se detectó una relación entre una hibernación más prolongada y mayor latitud, debido a la crudeza de la estación desfavorable, mientas que no se han detectado variaciones relacionadas con la altitud. Por último, como causas del abandono prematuro de las oseras hibernales, común en muchas poblaciones, se han identificado tanto las molestias humanas como la disponibilidad de alimento, natural o artificial, durante el invierno.

*Características de la osera y su entorno*. La elección de la osera es crucial para la condición física individual. En la revisión se describe como en distintas poblaciones las hembras son más fieles al área de hibernación, pero frecuentemente cambiando de osera. Esta suele ser una cavidad excavada o una cavidad natural, y compuesta de una entrada y una cámara conectada por un túnel, de dimensiones variables dependiendo de los materiales, pero suficientemente pequeña como para mantener una temperatura estable. El ambiente circundante a las oseras es muy variable, con factores a escala de paisaje y de microhábitat jugando un papel en su elección. En general se buscan características que contribuyan al aislamiento térmico, como la cubierta de nieve permanente y orientaciones en solana, así como la ocultación y el aislamiento por medio de una mayor cubierta vegetal y un emplazamiento alejado de molestias como las antrópicas, además de elevado y escarpado. Esto es particularmente aplicable a las hembras y aún más a las hembras preñadas, ya que hibernan por periodos más largos.

*Fisiología de la hibernación y potenciales costes energéticos*. Los osos pardos cuando hibernan están privados de agua y alimento, no orinan ni defecan y permanecen inmóviles durante periodos de hasta 7 meses, y disminuyen su temperatura corporal y gasto metabólico al mínimo para ahorrar recursos energéticos. Las adaptaciones fisiológicas que presentan les permiten hacer frente a la anuria, hiperlipidemia, osteoporosis, sarcopenia, síndrome metabólico, diabetes y patologías cardiovasculares, que en otros seres vivos serían letales o mermarían en gran medida su condición física, además de presentar un metabolismo basado en lípidos. Además, son capaces de permanecer en alerta y activar sus funciones vitales y movilidad rápidamente. Se han descrito variaciones entre poblaciones en función de la latitud o los recursos alimenticios disponibles, con variaciones de peso más elevadas en poblaciones norteñas. El metabolismo de los osos durante este periodo está basado en lípidos y son capaces de sobrevivir con concentraciones muye levadas de compuestos nitrogenados en el organismo, con el hígado y los riñones sin apenas funcionamiento. Apenas presentan pérdida de masa muscular o tejido óseo, lo que les permite mantener una condición física adecuada tras la emergencia. Por último, los osos pardos presentan implantación retardada del blastocito, lo que les permite dar a luz en lo más crudo del invierno, a fin de sincronizar la salida de la osera con un crecimiento óptimo de las crías.

Discusión. A fin de tener un conocimiento más detallado y preciso de este periodo de la vida del oso pardo, parece importante distinguir entre aquellos factores que condicionan la hibernación, como la disponibilidad de alimento, las condiciones climáticas y las necesidades metabólicas o reproductivas de los osos de sus consecuencias correlatos como los cambios fisiológicos o comportamentales. Un conocimiento preciso de la hibernación es crucial en el actual contexto de Cambio Global, donde muchas especies incluidos los osos tienen que hacer frente con variaciones climáticas cambiantes o más extremas y cambios en la disponibilidad de recursos. Estos desajustes fenológicos pueden afectar a la condición física, supervivencia y reproducción de los osos, que pese a ello exhiben cierta plasticidad para adaptarse a estos cambios.

### Capítulo II. El papel de las temperaturas primaverales en la fecha de emergencia de las oseras de las osas con crías del año en el suroeste de Europa.

Introducción. La hibernación es una estrategia de algunos animales para lidiar con condiciones ambientales desfavorables. Para que sea efectiva tiene que encuadrarse en un marco temporal en armonía con los factores ambientales. Sin embargo, los detonantes del inicio y fin de la hibernación so todavía poco conocidos, más en poblaciones donde los osos no hibernan cada año o no lo hacen todos los miembros de la población, al existir condiciones climáticas más suaves o alimento disponible. Conocerlos es particularmente importante en un contexto de clima cambiante como el actual En el oso pardo la única cohorte con hibernación obligada son las hembras gestantes, ya en ella tiene lugar el parto y la primera parte de la lactancia, por lo que es el grupo de osos más limitado en cuanto a flexibilidad de las fechas de hibernación. Es este capítulo se investigaron los detonantes de la emergencia de las oseras en 74 hembras con crías del año, esperando que una mayor temperatura, menor precipitación y mayor número de crías determinen una salida más temprana de la osera.

Material y métodos. Se estudiaron 74 eventos de salida de la osera invernal de hembras con crías del año recogidos entre 1995 y 2018. Se recopiló información sobre el número de crías de cada camada y sobre la temperatura máxima media, temperatura mínima media y precipitación media en los 30 días anteriores a cada fecha de salida, mediante modelos lineares mixtos para dilucidar si estos factores influían en las fechas de salida, y cómo. Además, se comparó la fecha media de salida con otros estudios similares a fin de comprobar el ajuste cronológico con el gradiente latitudinal descrito en el capítulo anterior.

Resultados. La fecha media de salida de la osera para las hembras con crías en la cordillera cantábrica fue el 28 de abril. Esta fecha concuerda con otras poblaciones a latitud similar u ocupando hábitats similares. El número de crías no parece influir en esta fecha. La única variable climática con efecto sobre la fecha de emergencia fue la temperatura máxima media de los 30 días anteriores a la emergencia.

Discusión. La variabilidad cronológica de la hibernación entre años y entre poblaciones es prueba de la plasticidad de los osos pardos. Esta cronología se encuentra en armonía con las condiciones climáticas, como demuestra el gradiente latitudinal con fechas de emergencia más tempranas según nos acercamos al ecuador. La relación inversa entre las temperaturas máximas en días previos a la emergencia y la fecha de emergencia había sugerida o reportada en otras poblaciones. No obstante, en una población habitando un área de clima templado y con disponibilidad de alimento durante el invierno esta fecha resulta temprana en comparación. Esta estrecha relación de las variables climáticas con la cronología de la hibernación hace patente la potencial sensibilidad de la especie a cambios en el clima como los actuales, y más en poblaciones como la cantábrica habitando áreas montañosas y/o en la periferia del rango de distribución, más sensibles a estos cambios. Posibles desajustes entre las fechas de inicio o final de la hibernación con el clima o con la fenología de los recursos alimenticios de los osos pueden tener consecuencias sobre el estado físico o la supervivencia de los individuos y condicionar la conservación de la especie.

## Capítulo III. Comportamiento de marcaje en el oso pardo europeo. Factores que determinan la selección y densidad de los árboles de marcaje.

Introducción. La comunicación a base de señales químicas es el principal canal de comunicación en muchas especies de mamíferos, no necesitando de la presencia conjunta de emisor y receptor, y que suele ser duradera. En especies solitarias, como el oso pardo, puede ayudar a mantener la estructura social. En esta especie se marcan gran variedad de sustratos a través de rascado, mordiscos, arañazos, pisadas, orinado, etc. El más conspicuo de ellos es el rascado contra árboles de marcaje, siendo as principales funciones el encontrar compañero potencial y comunicar dominancia entre machos. Estos árboles se reparten a lo largo del territorio osero y a veces son usados durante décadas, dando prueba de la importancia en la comunicación intraespecífica de la especie. En este capítulo se analizaron las características que determinan la selección de los árboles de marcaje, así como los factores que influyen en su abundancia, esperando que los osos seleccionaran aquellos árboles más conspicuos y que su abundancia aumentase en el centro del rango de distribución y fuera dependiente de la densidad de osos.

Material y métodos. Se analizaron las características dendrométricas en 101 árboles de marcaje y de sus respectivos controles, así como las características del entorno y la especie de árbol. Asimismo, se calculó un índice de abundancia linear de estos árboles en los transeptos realizados y se calculó la densidad de observaciones de oso alrededor de estos transeptos y su posición relativa dentro del rango de la población. Para el primer set de variables se construyó un modelo aditivo generalizado (GAM), mientras que para el segundo se construyó un modelo linear

Resultados. Los árboles de marcaje se localizaron preferentemente en exposiciones N y E, y el árbol más frecuentemente marcado respecto a su disponibilidad fue el abedul, seguido por las coníferas. Los árboles marcados presentaron mayor diámetro y tamaño del tronco, y se situaron más separados de otros árboles y cerca de caminos. Por otro lado, ni la densidad de observaciones ni la posición de los transeptos en el territorio osero tuvieron efecto sobre la abundancia linear de árboles de marcaje.

Discusión. Las características individuales seleccionadas por los osos se traducen en una mayor área para el rascado y una mayor facilidad de acceso al árbol, lo que se traduce tanto en mayor facilidad de deposición de la señal química como de recepción de la señal. Los árboles más seleccionados, abedules y coníferas, parecen serlo por diferentes motivos, los primeros por las propiedades químicas de su resina y los segundos por la facilidad de laceración de la corteza. La abundancia de árboles de marcaje no parece dependiente de la densidad ni de la posición en el territorio, siendo concordante con el carácter no territorial del oso pardo. Por último, se sugiere emplear estos árboles como nodos de localización o censo de individuos, lo que podría facilitar tareas de seguimiento y monitoreo de la especie.

**Capítulo IV. Marcaje visual en mamíferos probado por primera vez mediante manipulación del comportamiento de descortezado en osos.**

Introducción. La capacidad de comunicación visual ha sido frecuentemente subestimada en muchos grupos animales, posiblemente por nuestra escasa comprensión de la misma. Esto es particularmente cierto para los mamíferos, pese a que hay ejemplos de su uso como la coloración de algunas especies y pese a que presenta evidentes ventajas sobre otros canales, especialmente en especies solitarias. En el caso del oso pardo, la comunicación intraespecífica se ha considerado basada en el marcaje químico contra árboles o con las plantas de los pies. Sin embargo, la función de ciertas marcas de corteza arrancada que presenta algunos árboles no se ha explicado. Bajo la hipótesis de que estas marcas tienen una función visual, se realizó un experimento para comprobar y describir este comportamiento.

Material y métodos. En 20 árboles que presentaron estas marcas se realizó un experimento manipulativo en le primavera y verano de 2020. En él, se cubrieron estas marcas con fragmentos de corteza del mismo árbol, y se colocaron fragmentos similares en varios controles alrededor, esperando que si las marcas subyacentes tenían alguna función para los osos fueran éstos los fragmentos que retiraran y no otros. Delante de algunos árboles, para testar la especificidad del experimento, se colocaron cámaras trampa. Así mismo, se midió el contraste de color entre la mara y la corteza en las especies de árbol marcadas, por si existiera cierta selección por marcas más conspicuas (t-test.) Por último, se realizaron transectos en las proximidades de los árboles marcados para cuantificar la abundancia relativa de la especie marcada y testar si hubiese selección hacia ciertas especies, a través de un modelo linear.

Resultados. Se detectó la retirada de la corteza cubriendo las marcas visuales en 9 de estos árboles, en 3 de ellos produciéndose dos veces. No se retiró ninguno de los fragmentos de corteza colocados en los controles. Las cámaras colocadas mostraron que este comportamiento se llevó a cabo la primera vez que los osos visitaban el árbol y que fue realizado por machos adultos. No se encontró una diferencia de contraste entre especies ni selección preferente por ninguna de ellas, pero los árboles marcados pertenecían a especies poco abundantes

Discusión. Tras la retirada de los fragmentos colocados sobre las marcas visuales se probó la función comunicativa de las mismas. Pese a haberse sugerido que el arrancado de corteza pudiera depositar paralelamente saliva u otras sustancias con olor, la cantidad así depositada sería mínima comparada con el rascado o marcaje pedal, siendo su eficacia muy baja. Los individuos captados llevando a cabo este comportamiento fueron siempre machos adultos, lo que podría indicar una función de comunicación de dominancia entre machos relacionada con el tamaño del individuo, o bien de comunicación de características individuales de cara a la reproducción. La caracterización de estos árboles podría ayudar a monitorizar ciertos individuos en determinadas épocas del año, lo que permitiría la adquisición de una valiosa información para la conservación y gestión de la especie.

## Capítulo V. La influencia de la red de carreteras en la distribución espacial y la idoneidad de hábitat de un gran carnívoro en ambientes humanizados.

Introducción. Las carreteras son unas de las infraestructuras humanas más repartidas por el planeta, y afectan a los ecosistemas de muy diversas formas. Los animales con amplios dominios vitales, bajas tasas reproductivas y baja densidad poblacional, como los osos pardos, son particularmente vulnerables. Así, suele evitarlas o adaptar su comportamiento en el entorno de las carreteras a periodos de menor tráfico o visibilidad. En este capítulo se exploraron por un lado los efectos directos (sobre la localización de los osos) e indirectos (sobre la idoneidad de hábitat) de las carreteras, Se hipotetizó que las distancias a las carreteras serían menores en áreas con cobertura o cuando la carretera un fuese visible, con niveles bajos de tráfico y apara algunas cohortes que pudieran usarlas como refugio, además de en época de mayor ingesta de alimento. Por otro lado, se esperó que la idoneidad de hábitat para distintas cohortes en diferentes momentos del año variara.

Material y métodos. Para testar los efectos directos de las carreteras, se calculó la distancia a la carretera más cercana (en adelante, CMC) en 2722 localizaciones de osos recogidas entre 2000 y 2016 en relación a variables como la estación, la clase de oso, tipo de hábitat, visibilidad de la carretera y nivel de tráfico, además de variables topográficas. Con estas variables se construyeron modelos lineares. Además, se descartaron posibles sesgos según la fuente de las observaciones construyendo modelos separados para cada una y comparándolos entre sí. En cuanto a los efectos indirectos, se construyeron modelos de idoneidad de hábitat con y sin incluir la red de carreteras a través del software MaxEnt, para cada clase de oso en cada estación del ciclo vital de la especie.

Resultados. La distancia media de los osos a la CMC en la Cordillera Cantábrica fue de 968m. En los modelos elaborados para testar los efectos directos, el efecto de las variables sobre la distancia a la CMC fue de poca importancia, quedando fuera la rugosidad del terreno. En cuanto a los modelos de idoneidad de hábitat, las carreteras no atravesaron frecuentemente zonas con elevada idoneidad. Por otro lado, el efecto de la presencia de las carreteras sobre la misma tuvo escasa relevancia excepto para las hembras con crías del año durante la época invernal.

Discusión. Los resultados de este capítulo apuntan a una baja afección de la red de carreteras sobre la localización de los osos pardos cantábricos o sobre la idoneidad de su hábitat. Contrariamente a lo esperado, las variables consideradas en los modelos de efectos directos tuvieron poco efecto sobre la distancia a las CMC, y las carreteras no parecieron afectar significativamente a la idoneidad de hábitat, presumiblemente por hallarse construidas en entornos de por sí poco adecuados. Comparando estos resultados con los obtenidos en otros estudios realizados en Europa y Norteamérica, se hace patente la diferencia entre ambos continentes. Estas diferencias parecen obedecer a la diferente exposición a las actividades humanas y a su persecución, habiéndose extendido éstas durante milenios en Europa, en contraposición a lo ocurrido en Norteamérica, donde se reduce a 200 o 300 años. Se evidencia con ello la necesidad de considerar las características intrínsecas de cada población a la hora de diseñar medias de conservación y manejo de la especie, en base a la diferente respuesta frente a las carreteras que exhiben las distintas poblaciones.

## Conclusiones

1.- El impacto humano en los ambientes humanizados tiene consecuencias diversas sobre los ecosistemas, y ha obligado frecuentemente a las especies a adaptarse a estas presiones. Es particularmente relevante el caso de los grandes carnívoros, que son especialmente vulnerables debido a sus características biológicas y a la persecución histórica a la que se han visto sometidos. Un conocimiento más profundo de su comportamiento y la ecología en estos entornos es crucial para la correcta conservación y manejo de sus poblaciones.

2.- La hibernación es un periodo crítico en la vida de los osos pardos, que les permite superar periodos desfavorables. La cronología de la hibernación, variable entre clases de sexo y edad, es función tanto de variables ambientales como geográficas, existiendo un gradiente latitudinal en la misma. La elección de la osera invernal se basa en la selección de ciertas características de hábitat a gran y pequeña escala, y de ella puede depender la condición física o supervivencia de los individuos.

3.- La hibernación en el oso pardo supone un desafío metabólico en el que se han desarrollado una serie de adaptaciones fisiológicas únicas. Éstas les permiten soportar situaciones extremas como la privación de alimento o agua, la ausencia de excreción y niveles elevados de lípidos y compuestos nitrogenados en el organismo, así como prevenir patologías cardiovasculares y el deterioro de sus sistemas muscular y óseo.

4.- En cuanto a la hibernación, es importante distinguir entre factores próximos (condiciones ambientales) y últimos (procesos biológicos originados en el curso de la evolución), así como diferenciar adecuadamente los desencadenantes reales de la hibernación y otros factores correlacionados a éstos. Por otro lado, es necesario comprender mejor los periodos de hiperfagia y pre-hibernación de la especie, estrechamente relacionados con la hibernación y de los que depende su éxito.

5.- La fecha de finalización de la hibernación de las osas con crías en la Cordillera Cantábrica depende de la temperatura máxima en los días previos. Aquí, la cronología de la hibernación es variable interanualmente y se encuentra en armonía con el gradiente latitudinal existente entre diferentes poblaciones de oso pardo, lo que prueba la plasticidad exhibida por la especie y su capacidad de adaptación.

6.- Habida cuenta del efecto de las temperaturas sobre la cronología de la hibernación, es imprescindible comprender e investiga los posibles efectos del Cambio Global sobre el oso pardo, como potenciales desajustes desajuste entre la cronología de la hibernación y la disponibilidad de alimentos, que pueden tener efectos sobre la condición física de los individuos y con el incremento de conflictos con el ser humano. Esto es particularmente relevante en aquellos lugares donde se prevé que estos cambios ambientales tengan un mayor impacto, como en la Cordillera cantábrica.

7.- La comunicación química basada en la deposición de olores en los árboles de marcaje es la principal vía de comunicación intraespecífica en los osos pardos. La selección de estos árboles obedece a características individuales y de entorno de los mismos, que incrementan la conspicuidad de la señal y la facilidad de deposición y recepción de la información, más que a variables poblacionales o de localización geográfica dentro del rango de la especie.

8.- La comunicación visual ha sido pasada por alto en muchos grupos animales, incluidos los mamíferos. Sin embargo, especies como el oso pardo a través de las marcas en la corteza de los árboles, la emplean para la comunicación intraespecífica. Este canal de comunicación parece tener un uso más restringido que el marcaje químico, estando relacionado con la comunicación de dominancia entre machos durante la época de reproducción de la especie.

9.- El uso de los árboles de marcaje (químico y visual) como nodos de comunicación en las poblaciones oseras puede suponer una valiosa herramienta de monitorización y gestión de la especie. Los censos poblacionales o el seguimiento de individuos concretos a través de éstas localizaciones permitirían una colección de datos más eficiente y completa y por tanto generar información de mayor calidad con un menor esfuerzo.

10.- Las carreteras y el tráfico tienen un profundo impacto sobre los ecosistemas y las especies, incluido el oso pardo. Pese a ello, en aquellas poblaciones habitando desde hace milenios un entorno humanizado, como la cantábrica, los osos parecen presentar cierta habituación y tolerancia a la presencia humana y sus infraestructuras y actividades. Estas adaptaciones parecen estar menos presentes en poblaciones que ocupan entornos con escasa presencia humana o donde ésta es reciente.

11.- A fin de lograr una conservación y gestión adecuada de las poblaciones de grandes carnívoros, y por ende de la coexistencia con los seres humanos, es preciso tener en cuenta las particularidades de cada población, especialmente de aquellas que habitan entornos humanizados. estas particularidades de su comportamiento y ecología, y su respuesta y adaptación frente a las presiones humanas depende de la exposición histórica a los seres humanos y sus actividades.

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